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JOURNAL OF ANATOMY

THE ACTION OF REPEATED DOSES OF X-RAYS UPON THE DEVELOPING CHICK EMBRYO[1]

By HECTOR A. COLWELL, M.B., D.P.H.,
REGINALD J. GLADSTONE, M.D., F.R.S.E.,
and CECIL P. G. WAKELEY, F.R.C.S. (Eng.)
University of London, King's College Hospital

INTRODUCTION

It was not until nearly ten years after the first demonstration of the X-rays in 1895 that work dealing with their action upon developing forms was published. The earliest experiments were those of Perthes upon the ova of *Ascaris megalocephala*, which appeared in 1904; broadly stated, he found that exposure to the rays resulted in delayed development and the production of abnormal forms.

Bordier in 1905 exposed young larvae of the common silkworm and found inhibitory effects upon subsequent development, as did also Hasebroeck, while experimenting upon young forms of other species of Lepidoptera. Hastings, Beckton and Wedd, in a series of observations carried out upon silkworms from 1909 to 1911, which extended over three cycles of their life history, observed generally an inhibitory effect of the rays upon development.

In 1904 Gilman and Baetjer observed temporary stimulation in the development of the eggs of *Amblystoma* as a sequel to irradiation, but in spite of this the resulting forms were abnormal.

Bardeen in 1907–1911 published an extended series of observations upon the action of the X-rays upon amphibian ova, paying particular attention to the susceptibility of the embryos at different stages of development. For this purpose amphibian ova—toad and frog—offer many advantages, since artificial fertilisation of ova removed from the female animal can be readily effected by the addition of an emulsion of the carefully "teased" testis. Bardeen's experiments comprised irradiation of unfertilised ova, of spermatozoa, and of fertilised ova at different stages of development. He found that spermatozoa, unimpregnated ripe ova and recently fertilised ova were highly susceptible to the rays, that their susceptibility decreases in the second hour after fertilisation, rapidly increases to a maximum in the earlier cleavage stages, and greatly decreases during the stage of gastrulation. Bardeen's results are given with remarkable fullness and detail and to be fully appreciated the original memoirs must be consulted.

[1] The expenses of this research were partly defrayed by a grant from the Medical Research Council.

Passing now to the consideration of chick-embryos, the first experiments upon the effects of exposure to the X-rays were those of Gilman and Baetjer in 1904. Here the observers recorded an initial acceleration of development, followed by retardation and the production of abnormal forms. Bordier and Galimard in 1905 obtained inhibition of development as a result of exposure, as also did Gaskell in 1911.

In the case of developing mammals, the results of exposure to the X-rays were in all cases found to be deleterious, whether the exposure took place before birth (by exposure of pregnant females) or whether newly born animals were irradiated. The details of experiments of this nature are given, and the results summarised, in a paper by Walter which appeared in 1912.

Before entering upon the details of our present lines of experiment, it may not be out of place to offer a few remarks upon the nature of the X-rays, and their relations to other forms of radiation.

The X-Rays.

Recent investigations have shown that the X-rays consist of electromagnetic waves similar in character to rays of light and ultra-violet rays. From these they differ in having much shorter wave lengths. We are now acquainted with a complete series of undulations, comprising among others the Hertzian waves used in wireless telegraphy, the rays which produce heat, the visible rays, the ultra-violet rays, the X-rays and the gamma rays of radium. From the analogy of such a series of undulations to the visible spectrum, its representation is often referred to as the spectrum of electromagnetic waves, although only a part—and that a very small part—is capable of affecting the retina so as to produce the sensation of light. The unit of measurement commonly used by physicists for describing wave lengths of these undulations is known as the Ångstrom unit (A.U.) and measures one ten thousand millionth part of a metre, and is also often referred to for the sake of brevity as a "tenth metre." This unit is also expressed as 10^{-10} metre or 10^{-8} centimetre.

Now the visible spectrum from deep red to extreme violet, comprises rays which lie between the limits 7200 and 4000 A.U.; it will be seen that the wave length of the shortest member of the series is about one-half of that of the longest. Such a series of waves are spoken of as forming an "octave" of the spectrum, and thus the visible rays comprise almost one octave of the spectrum of electromagnetic waves. The next group of radiations beyond the visible spectrum consist of undulations of gradually decreasing wave lengths from the ultra-violet rays; these extend over several octaves. Following them is a region which, thanks to the researches of J. J. Thomson, Millikan, Richardson and others has recently been charted. If we reckon rays of the visible spectrum as constituting the first octave now under consideration, well-defined X-rays make their appearance in the tenth octave. X-rays of longer wave lengths than this have been detected in the intervening octaves but, owing to the fact that they are very easily absorbed by matter, the study of their

properties has been rendered extremely difficult. The X-rays which are in common use start about the fourteenth octave, they extend over about three octaves and overlapping them and eventually extending beyond them are gamma rays of radium. The wave length of the most penetrating X-ray yet produced is about $0{\cdot}06 \times 10^{-8}$ cm., while the most penetrating gamma ray has a wave length about $0{\cdot}01 \times 10^{-8}$ cm.

Thus the X-rays increase in penetrating power as their wave lengths diminish; the "softer" rays, or rays of greater-wave-length will be stopped by, e.g., sheets of metal which allow rays of shorter wave length, or "harder" rays to pass through. Not only is the thickness of the metal screen a factor in stopping the passage of the radiations, but the material of which it consists. Metals of high atomic weight have normally greater stopping powers than metals of low atomic weight.

Now the beam of X-rays from an X-ray tube is never homogeneous, the rays emitted consist of a mixture of radiations of different wave lengths, some "harder" and some "softer." By using a series of metal screens of varying thickness we can gradually cut out the rays of greater wave length while those of shorter wave length are allowed to pass.

This property of metallic screens is made use of in the therapeutic application of the rays and screens of aluminium varying from half a millimetre up to six or eight millimetres or more are interposed between the X-ray tube and the object irradiated according to the requirements of the particular case.

If now we imagine the tube to be running at a fairly constant intensity so that the total out-put of X-rays for a given time is a more or less fixed quantity, the interposition of the screens of gradually increasing thickness will diminish the total amount of rays received by the object irradiated. Thus an object exposed to the rays for two minutes without any screen will receive more total rays, than if a screen be interposed. We are therefore faced with the problem of how to obtain approximately equal doses of radiation when the softer X-rays are cut out by the screen.

In ordinary X-ray therapy the unit of radiation used is very commonly what is known as the Sabouraud-noire pastille dose. It is open to a good many objections but its simplicity of application has secured its extensive use while it is moreover based upon practical therapeutic experience. In brief it consists in the observation of the colour changes produced in a paper disc impregnated with barium platinocyanide as the result of exposure to X-rays. These discs or "pastilles" (which are also sensitive to light, heat and other physical agencies, so that they have to be kept under fairly stringent conditions) are normally of a pale apple green colour. With exposure to X-rays this tint gradually changes to a yellowish-brown according to the amount of irradiation. The unit known as a "pastille dose" (1 P.D.) was originally determined experimentally by Sabouraud who compared the intensity of irradiation necessary to produce a definite erythema of the skin with the colour changes produced in one of these "pastilles" or discs. A dose of X-rays which just

produced cutaneous erythema was found to produce a reasonably constant tint in the barium platinocyanide disc and this amount of irradiation forms the unit of pastille dose (P.D.).

Now if screens are interposed between the X-ray tube and the object irradiated, and the disc is placed on the side of the screen remote from the tube, it will, within certain limits, be affected by the total rays passing irrespective of their hardness and its colour changes will depend solely upon the rays which have filtered through the screen. Obviously with increasing thickness of the screens, greater duration of exposure will be necessary to produce the standard change in the pastille.

The colour changes produced by the rays in the platinocyanide disc are estimated by comparing the tints produced with a series of pieces of standard coloured glass in a simple tintometer, whereby such subdivisions of the pastille dose as four-fifths ($\frac{4}{5}$ P.D.), half ($\frac{1}{2}$ P.D.) or a quarter of a pastille dose ($\frac{1}{4}$ P.D.) can be judged.

The Present Experiments

The object in our present series of experiments was to ascertain the action of rays of different degrees of "hardness" upon developing tissues. The chick embryo was selected as the subject of experiment and a series of 36 fertilised eggs were subjected daily to irradiation for a period of 8 days. These were divided into four series which received one pastille dose (1 P.D.), four-fifths ($\frac{4}{5}$ P.D.), one half ($\frac{1}{2}$ P.D.) and one quarter of a pastille dose ($\frac{1}{4}$ P.D.) respectively daily. The same series of screens were used in all the experiments; they were aluminium screens of one half millimetre, one millimetre, and two millimetres, in thickness. This is epitomised in the following table.

Thickness of aluminium screen	½ mm.	1 mm.	2 mm.
Series 1. 1 P.D.	3 eggs	3 eggs	3 eggs
Series 2. ⅘ P.D.	3 „	3 „	3 „
Series 3. ½ P.D.	3 „	3 „	3 „
Series 4. ¼ P.D.	3 „	3 „	3 „

All irradiated daily for 8 days

The apparatus used was one of the ordinary coils used in the therapeutic X-ray department of King's College Hospital, working with a spark-gap of 6 inches. The current through the primary coil was about 4 amperes at 100 volts, while the current through the secondary was 2 milliamperes. A Coolidge tube was used and the anticathode was 4 inches from the pastille which was, of course, placed on the side of the screen away from the tube. The eggs were covered with a layer of cotton wool and placed in a cardboard box for irradiation.

The first irradiation was given before the eggs were placed in the 37° C. incubator; immediately it was completed they were incubated and only removed for the short time needful for their daily exposure for 8 days. The weather was warm at the time and the eggs were kept covered with cotton

wool during their transit to and from the incubator as well as during incubation and irradiation. They were turned over daily.

On the eighth day the eggs were opened and the embryos carefully transferred to Muller's fluid to which 5 per cent. glacial acetic acid had been added. This fluid was changed daily for one week when the embryos were passed through ascending strengths of alcohol, then through xylol and embedded in the usual way. Serial sections were then cut of each embryo.

Series 1. 1 P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(*a*) ½ mm. filter	(*b*) 1 mm. filter	(*c*) 2 mm. filter
(1) Undeveloped	(1) Undeveloped	(1) Undeveloped
(2) Undeveloped	(2) Undeveloped	(2) Undeveloped
(3) Dead and measured 4 mm.	(3) Dead and measured 4 mm.	(3) Dead and measured 4 mm.

Series 1 (*a*). Daily dose, 1 P.D. through ½ mm. aluminium filter for 8 days.

The only specimen which showed any signs of development was dead, its greatest length was 4 mm. There is marked maceration of the tissues; this no doubt is due to decomposition changes after death. The epithelium is shed both from the surface ectoderm and from the alimentary and respiratory tracts. The central nervous system is completely disintegrated. In the cardio-vascular system the blood shows as a fibrinous clot in which no blood corpuscles can be distinguished. The endothelial lining of the vessels is separated from the muscular wall, but appears as a continuous membrane.

Series 1 (*b*). Daily dose, 1 P.D. through 1 mm. aluminium filter for 8 days. The findings were identical with those obtained in Series 1 (*a*).

Series 1 (*c*). Daily dose, 1 P.D. through 2 mm. aluminium filter for 8 days.

Here again only one specimen shows any signs of development and its greatest length measures 4 mm. The surface epithelium and that of the alimentary and respiratory tracts is again observed to be shed and disintegrated, doubtless due to post-mortem changes. As regards the central nervous system the walls of the cerebral vesicles are seen to be markedly folded and the tissues macerated. This is probably due to post-mortem changes. The mesenchyme is denser and the tissues less broken up than in the former specimens.

In the genito-urinary tracts signs of development had proceeded further than Series (*a*) and (*b*), and tubules and glomeruli can be recognised in the mesonephros. As regards the cardio-vascular system, red blood corpuscles are recognisable in places and the heart is developed but its walls disintegrated.

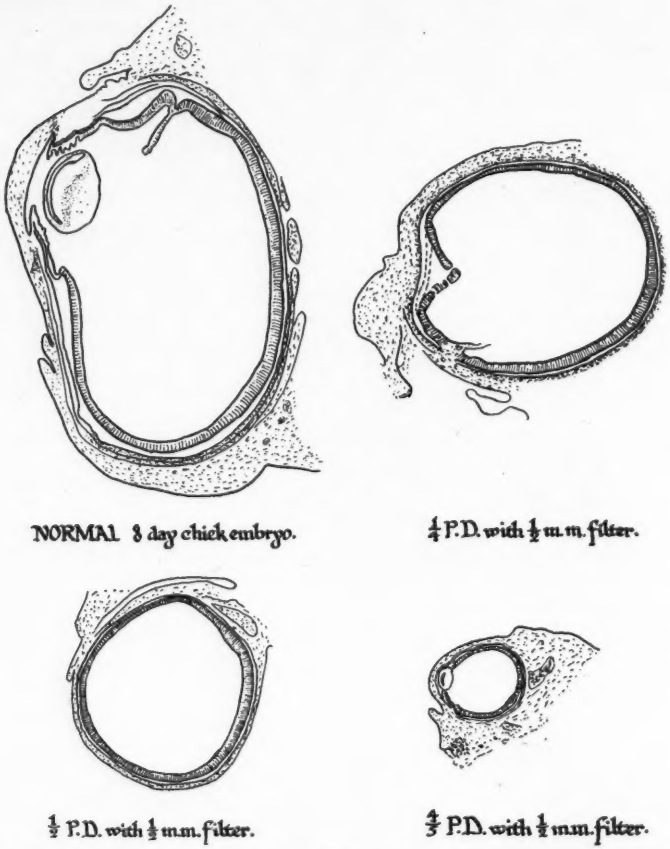
Series 2. ⅘ P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(*a*) ½ mm. filter	(*b*) 1 mm. filter	(*c*) 2 mm. filter
(1) Undeveloped	(1) Undeveloped	(1) Undeveloped
(2) Trace of embryo apparently of 48 hours development	(2) Dead and measured 10 mm.	(2) Dead and measured 4 mm.
(3) Living and measured 8 mm.	(3) Living and measured 10 mm.	(3) Living and measured 12 mm.

Series 2 (*a*). Daily dose $\frac{4}{5}$ P.D. through $\frac{1}{2}$ mm. aluminium filter for 8 days.

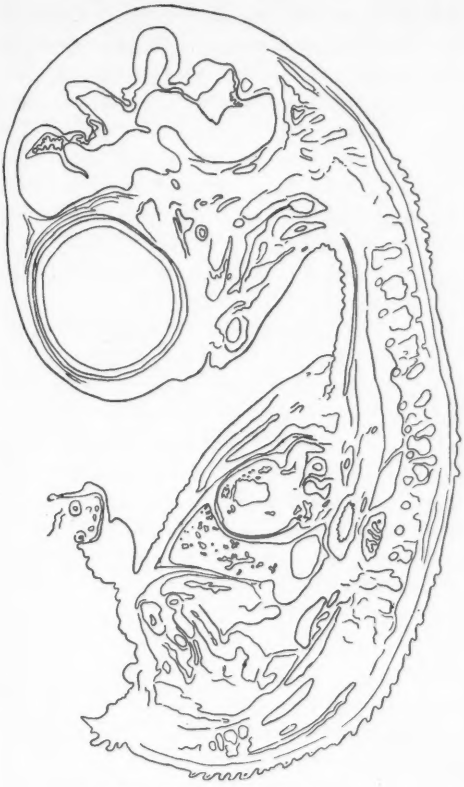
Of the three eggs examined one was undeveloped, one showed a trace of an embryo apparently of 48 hours' development while the third was alive and measured 8 mm. in its greatest length; this was the one selected for examination.



ectio through the greater diameter of the eyeball of a normal chick embryo at the 8th day for comparison with chick embryos at a similar age which have been subjected to the influence of X-rays.

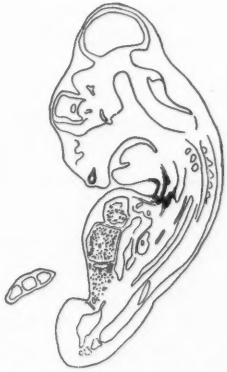
The surface ectoderm is recognisable as a distinct layer although nuclei and cell outlines are indistinct; this applies also to the epithelium of the alimentary and respiratory tracts.

The epithelium of the optic vesicles and retina are differentiated and not separated, as in the previous cases, from the underlying tissues, and there is also a further differentiation of the cell elements of the mesenchyme. Although

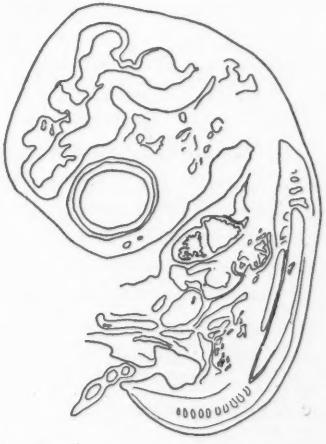


8 days, 22 mm. ×5. Control.

8 days, 16 mm. ×5. ¼ P.D.
1 mm. filter



8 days, 11 mm. ×5. ¼ P.D.
2 mm. filter.



8 days, 13 mm. ×5. ½ P.D. 1 mm. filter.

the embryo is less than half the size of a normal 8 day chick embryo, the optic vesicle and lens are only one quarter of the normal size, and there seems to be considerable difference in the relative sizes of other individual organs, such as the kidney and lungs. In the case of the eye the differentiation of the various layers of the retina is not nearly so advanced as in the normal condition. The differentiation of the sclerotic cartilage of the orbit has not taken place, while the iris and ciliary body are not differentiated from the sensitive part of the retina. The pigment of the ensheathing layer of the optic cup is present but the granules are neither so numerous nor so dark as in a normal 8 day chick embryo. There is no indication of penetration of the rods and cones through the external limiting membrane of the retina.

As regards the other organs individual parts are all easily distinguished.

The cardio-vascular system appears normal as are also the amnion, the wall of the yolk sac and the allantois. There is no sign of the development of feathers.

Series 2 (*b*). Daily dose, $\frac{4}{5}$ P.D. through 1 mm. filter for 8 days.

Of the three eggs in this series one was undeveloped, one was dead, while the third was alive; serial sections were made of the two latter specimens.

(1) The dead specimen had attained the length of 10 mm.; the tissues were macerated and the epithelium was for the most part separated from the underlying tissues. The central nervous system showed folding and in places was disintegrated. Death must have taken place at the commencement of the fifth day.

(2) The living specimen was about half the size of a normal 8 day chick and measured 10 mm. in its greatest length. The surface epithelium forms a distinct layer and is not separated from the underlying tissues. The cell outlines are indistinct and the nuclei are not deeply stained. The epithelial tissues are differentiated in the central nervous system, alimentary and respiratory tracts, as are also the mesothelium of the genito-urinary organs and coelom, and the endothelial lining of the blood vessels. The blood corpuscles are well formed and their nuclei well stained. The optic vesicle and lens show the same degree of development and differentiation as are present in the specimen in Series 2 (*a*) ($\frac{4}{5}$ P.D. $\frac{1}{2}$ mm.). No indication of the growth of feathers is present.

Series 2 (*c*). Daily dose, $\frac{4}{5}$ P.D. through 2 mm. aluminium filter for 8 days.

Of the three eggs one was undeveloped, one was dead (it corresponded to a 72 hour chick), while the third was living and had attained the length of 12 mm.

The surface epithelium forms a distinct layer in which the cell outlines can be distinguished. The structure of the central nervous system is highly differentiated as is also the epithelium of the respiratory, alimentary and genito-urinary systems. The development of the cardio-vascular and other systems has reached that of an 8 day chick embryo, although the size is only that of a 5 day embryo.

The genital gland, although of the same size as that of a $5\frac{1}{2}$ day embryo, can already be recognised as an ovary. No follicles of feathers are present.

Series 3. ½ P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(*a*) ½ mm. filter	(*b*) 1 mm. filter	(*c*) 2 mm. filter
(1) Living and measured 13 mm.	(1) Living and measured 13 mm.	(1) Undeveloped
(2) „	(2) „	(2) Living and measured 13 mm.
(3) „	(3) „	(3) „

Series 3 (*a*). Daily dose, ½ P.D. through ½ mm. aluminium filter for 8 days.

All three embryos were alive in this series of which one only was sectioned; it had attained the length of 13 mm.

This embryo had reached the stage of an 8 day chick although it had only attained the size of one of the sixth day.

The surface epithelium is a distinct layer, its microscopical appearance is good and cell outlines can be distinguished easily. The histology of the central nervous system is good and highly differentiated. In the optic vesicle the outer extremities of the rods and cones are not seen to be projecting through the external limiting membrane as they do in the normal condition at this age. Pigment is present in the outer pigment layer of the retina. The epithelium of the cardio-vascular, alimentary, respiratory and genito-urinary tracts is normal.

No indication of follicles of feathers is present.

Series 3 (*b*). Daily dose, ½ P.D. through 1 mm. aluminium filter for 8 days.

All the three embryos were alive in this series of which only one was sectioned. This embryo had attained the development of an 8 day chick, but only measured 13 mm. in its greatest length. The histological appearances were identical with those of the preceding specimen.

Series 3 (*c*). Daily dose, ½ P.D. through 2 mm. aluminium filter for 8 days.

Of this series one embryo was undeveloped, while the other two had attained the length of 13 mm.

In these specimens the histological differentiation was better marked than in any other of the previous specimens, the cell outlines being more clearly marked and the nuclei more distinct.

With regard to the central nervous system; in the pigment layer of the retina, granules could be distinguished, otherwise the specimens presented much the same appearances as in Series 4 (*a*) (¼ P.D. ½ mm.).

Series 4. ¼ P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(*a*) ½ mm. filter	(*b*) 1 mm. filter	(*c*) 2 mm. filter
(1) Not fertilised	(1) Living and measured 15 mm.	(1) Not fertilised
(2) Living and measured 15 mm.	(2) „	(2) Living and measured 15 mm.
(3) „	(3) „	(3) „

Series 4 (*a*). Daily dose, ¼ P.D. through ½ mm. aluminium filter for 8 days.

In this series one egg was found to be unfertilised; in the remaining two the embryos were alive and had attained the length of 15 mm. The histology

was good and the cell outlines and nuclei showed clearer differentiation than in any of the preceding specimens. There was a definite indication of developing feathers on the dorsal aspect of the embryo. This is the first embryo which showed any indication of developing feathers. Although the specimen was dwarfed it exhibited no other deviation from the normal type.

Series 4 (*b*). Daily dose, $\frac{1}{4}$ P.D. through 1 mm. aluminium filter for 8 days.

In this series all embryos were alive and measured 15 mm. in greatest length.

As regards both size, histology and development these specimens presented appearances identical with those seen in Series 4 (*a*) $\frac{1}{4}$ P.D. $\frac{1}{2}$ mm.

Series 4 (*c*). Daily dose, $\frac{1}{4}$ P.D. through 2 mm. aluminium filter for 8 days.

In this series one of the eggs was found to be unfertilised, the remaining two were alive and measured 15 mm.

The only difference observed between the embryos in this series and those in the two preceding series ($\frac{1}{4}$ P.D. $\frac{1}{2}$ mm. and $\frac{1}{4}$ P.D. 1 mm.) was that the feathers showed a more advanced stage of development, although this was still less than normal.

Summary of Results.

1. The rays were found to have an inhibiting effect in all cases. The greatest length of a normal chick embryo at the eighth day of development was found to be 22 mm.; of the experimental series the maximum lengths obtained were as under:

Series 1 (*a*)	1	P.D.	$\frac{1}{2}$	mm.	filter =	4 mm.
„ 1 (*b*)	1	„	1	„	„ =	4 „
„ 1 (*c*)	1	„	2	„	„ =	4 „
„ 2 (*a*)	$\frac{4}{5}$	„	$\frac{1}{2}$	„	„ =	8 „
„ 2 (*b*)	$\frac{4}{5}$	„	1	„	„ =	10 „
„ 2 (*c*)	$\frac{4}{5}$	„	2	„	„ =	12 „
„ 3 (*a*)	$\frac{1}{2}$	„	$\frac{1}{2}$	„	„ =	13 „
„ 3 (*b*)	$\frac{1}{2}$	„	1	„	„ =	13 „
„ 3 (*c*)	$\frac{1}{2}$	„	2	„	„ =	13 „
„ 4 (*a*)	$\frac{1}{4}$	„	$\frac{1}{2}$	„	„ =	15 „
„ 4 (*b*)	$\frac{1}{4}$	„	1	„	„ =	15 „
„ 4 (*c*)	$\frac{1}{4}$	„	2	„	„ =	15 „

2. From the above it is seen that with the exception of the second series the screening had little effect on the total growth of the embryos.

3. The tissues most affected by radiations were the surface ectoderm; feathers were not seen in any of the series except in Series 4; here it was noticed that when using a 2 mm. aluminium filter, they had attained further degree of development than in those protected by a 1 mm. filter; these again were slightly more advanced than those only protected by the $\frac{1}{2}$ mm. filter.

4. *The central nervous system and eye.* Throughout the whole of the first series (1 P.D.) the central nervous system and eye showed such a degree of disintegration, partly perhaps due to post-mortem changes, that any deductions were impossible. It was noticed that the ill differentiated epithelium of the optic vesicle and that of the retina were separated from the subjacent tissues.

In the second series ($\frac{1}{5}$ P.D.) it was noticed that the epithelium of the optic vesicles and retina was differentiated and not separated from the underlying tissues. As regards the retina the differentiation of its various layers is not very advanced.

In the third series ($\frac{1}{2}$ P.D.) the histology of the central nervous system was good and highly differentiated and pigment could be seen in the outer pigment layer of the retina.

In the fourth series ($\frac{1}{4}$ P.D.) the central nervous system and retina had attained the degree of differentiation of a normal 8 day chick embryo but they were smaller in size.

5. *The cardio-vascular system.* In Series 1 (1 P.D.) the first signs of blood corpuscles were first noticed in the specimen which had been protected by a 2 mm. screen; the heart was formed, but its tissues disintegrated in all members of this series.

In Series 2 ($\frac{1}{5}$ P.D.) and subsequent series up to $\frac{1}{4}$ P.D. the heart and blood vessels appeared normal except for diminution in size.

General Conclusions

In chick embryos irradiated immediately before incubation and then subjected to daily irradiations for several days the following results were obtained. The action of the rays was, as said, in all cases inhibitory, irradiated embryos being invariably smaller than controls. *Within the limit of radiation investigated*, the effects seem rather to depend upon the total amount of radiation reaching the embryo than upon its quality or "hardness." In the series which received a full pastille dose six out of nine specimens examined showed no sign of development at all.

As regards the susceptibility of individual tissues and structures to these conditions, this was found to be most marked in the surface ectoderm, the central nervous system and the eye.

Further experiments have yielded results which indicate that exposure of embryos which have been allowed to incubate normally for a period of 90 hours and which have then been exposed to X-rays for three successive days produces in some cases a certain degree of stimulation as indicated by a slight increase in size. The authors hope to give a detailed description of these experiments in a subsequent paper.

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ABNORMAL LEFT CORONARY ARTERY OF OX HEART COMMUNICATING DIRECTLY WITH THE CAVITY OF THE LEFT VENTRICLE NEAR THE APEX

By CHARLES REID, M.A., B.Sc., M.B., Ch.B.

From the Physiological Laboratory, University of Aberdeen

A hitherto undescribed abnormality was observed in an ox heart received by the above department about the end of October, 1921. Externally, the heart showed at the apex of the left ventricle a circular cyst-like structure. The heart was then held, with the cut end of the aorta pointing upwards, under a tap of running water. The water was allowed to run gently into the aorta, and the cyst-like structure was observed to bulge with fluid. On closer examination, a tubular vessel of arterial type about the calibre of one's middle finger was observed in the interventricular groove between the aorta and this structure at the apex of the left ventricle. This vessel appeared to follow the usual course of the descending branch of the left coronary artery towards the apex of the heart. It should be noted that, anteriorly, over the cyst-like dilatation, the ventricular muscle was quite deficient, and seemed to have been displaced by this abnormal structure.

Heart: weight with attachments of great vessels and fat, 95 ounces.

[Weight of another normal ox heart, 89 ounces.]

Length of heart, 24 cm.
Width of heart, 19 cm. } during rigor.

The auricles looked normal. The thickness of the walls of the left ventricle during rigor was about 5 cm. and did not differ materially from that of the normal ox heart.

With regard to the previous history and health of the animal, the following facts were obtained:

Age, rising 3 years old. Never off feed; very good feeder; always active; walked to sale from the farm ($\frac{3}{4}$ mile). Proportion of beef to live weight, fair average.

The calibre and thickness of the walls of the following vessels are given for the purpose of comparison:

Vessel	Calibre	Thickness of wall
Aorta (about 8 cm. beyond the valves) ...	3·0 cm.	8 mm.
Innominate artery (at its origin)	1·75 „	5 „
Abnormal artery (at its origin above the cusp)	1·5 „	1·5 „

It will be observed that, while the calibres of the innominate artery and abnormal artery are approximately equal, the wall of the latter is much thinner than that of the former.

Further dissection showed that this abnormal vessel arose about 1·25 cm. above the middle of the left posterior cusp of the aortic valve. The tip of the middle finger could be inserted into the vessel at its origin. A coronary artery, smaller in size, arose above the anterior cusp, but no artery arose above the right posterior cusp. In the normal ox heart the calibres of the two coronaries differ considerably, the left being the larger, but the normal left coronary artery did not admit the tip of the middle finger.

No other abnormal opening was noted at the base of the aorta. The aortic wall was healthy and the aortic valves appeared healthy, and, when tested by means of a stream of water directed into the cut end of the aorta, proved competent.

The abnormal vessel passed forward between the left auricular appendix and the pulmonary artery. The first branch came off the main vessel about 3·5 cm. from the cusp, and ran transversely outwards in the left auriculo-ventricular groove. Its calibre appeared similar to that of the normal right coronary artery. This branch was evidently the transverse branch of the left coronary artery and was of normal size.

The abnormal vessel passed along the interventricular septum giving off numerous small branches to the septum without any marked diminution in calibre until it reached just above the apex of the left ventricle anteriorly where it dilated into a cyst-like structure roughly conical in shape with its base anterior and its apex on a level with the inner surface of the left ventricle. With regard to the dimensions of the above structure, the diameter of the base of the cone was about 7 cm. while the height of the cone was about 6 cm. It will be noted that the height of this structure is practically equal to the thickness of the wall of the left ventricle.

The wall of the cone-shaped structure appeared similar in structure to the wall of the abnormal vessel but slightly thinner. It was lined by smooth endothelium, and its base was quite uncovered by cardiac muscular fibres, being apparently in direct relationship with the pericardium. The rest of the wall of the cone-shaped structure was attached firmly to the muscle of the left ventricle throughout its entire thickness.

The walls of the abnormal vessel and the dilated portion were apparently continuous. Anteriorly, where the wall of the dilated portion was not attached to the wall of the ventricle, the epicardium passed directly on to the wall of the dilated portion. At first, the union was not firm, the two being held together by loose tissue, but at a distance of about 2 cm. from the place where the ventricular muscle became deficient the wall of the dilated portion and the epicardium became fused apparently into one.

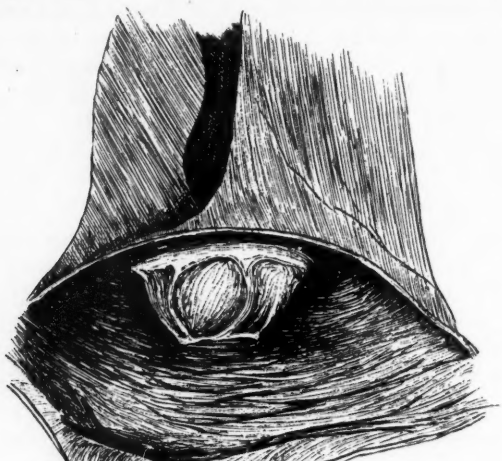
The cavity communicated directly with the left ventricle near its apex by a circular aperture, which was sufficiently large to admit the middle finger, and was guarded by a valve-like structure. Examination showed that the latter consisted of:

(1) an inner fibrous ring, diameter 1·5 cm., forming the circumference of the aperture,

(2) an outer fibrous ring, 3·5 cm. in diameter,

(3) thin fibrous material covered by smooth endothelium, stretching between the two rings and thickened by six or seven fibrous bands running radially between the two circular fibrous rings.

No other abnormality, developmental or acquired, was noted in the right or left chambers of the heart. The interventricular septum did not appear to be in any way abnormal, and the coronary veins both right and left were small. They did not appear to be enlarged on either side of the heart.



Lateral view of valve-like structure between cavity of left ventricle above and cyst-like dilatation below.

From its origin and course, this abnormal vessel was taken to be a left coronary artery—the abnormality affecting more particularly the descending branch of the left coronary artery. The dilatation of the terminal portion of the vessel at the apex was difficult to explain. This dilatation might have been due wholly to the developmental abnormality, or it might have been acquired mainly. If the latter supposition was correct, the dilatation would have been of the nature of an aneurismal dilatation. Support might be lent to this view by the fact that, when the dilated portion was distended with water, it was noted that at two or three places the wall was much thinned. The distension might have been brought about by the escape of blood from the left ventricle throughout the greater part of systole before the opening between the cavities of the left ventricle and the dilated part was closed by the contraction of the left ventricle towards the end of systole.

Developmentally, no explanation of the abnormal coronary and communication with the left ventricle has been suggested.

The only related case on record was described by Mr H. Blakeway in the *Journal of Anatomy*, vol. LII, p. 354. The heart in this case—a child which lived 36 hours—had amongst other abnormalities no direct communication between the left ventricle and the aorta, but an indirect one by means of the anterior interventricular branch of the left coronary artery. Mr Blakeway considered the question of the possibility of the origin of the abnormal communication between the aorta and the left ventricle as being due to some developmental peculiarity of the bulbus cordis. He, however, rejected this consideration.

The actual course taken by the blood in the abnormal ox heart forms an interesting speculation. Before the heart went into rigor, the left ventricle was artificially compressed above the apex to imitate systole, and at the same time a stream of fluid under pressure was directed against the pseudo-valvular opening by means of a tube introduced through the aorta past the aortic valves. Practically no fluid escaped into the dilated part. Again, fluid was allowed to run into the aorta. The aortic valve being competent, most of the fluid passed along the abnormal channel. The fluid entered the cavity of the left ventricle (the left ventricle being empty) through the pseudo-valvular opening, if the left ventricle was not compressed.

It would appear that during the greater part of systole leakage took place directly from the left ventricle to the dilatation at the apex. In all probability, the opening between the left ventricle and the dilated portion would not be closed by ventricular contraction except towards the end of systole. During diastole, unless the pseudo-valvular structure acted as an efficient valve, there must have been free communication between the aorta and the interior of the left ventricle, and the diastolic pressure in the abnormal vessel and in the interior of the left ventricle must have been equal to the pressure in the aorta. After the wall of the distended part at the apex of the left ventricle was laid open, a strong stream of fluid was directed against the valve-like structure. It appeared to act as an efficient valve except when the left ventricle was distended or relaxed.

As bearing on the accepted relation between increased diastolic intraventricular pressure and dilatation and the striking development of dilatation and hypertrophy in aortic regurgitation in man, it is noteworthy that in this ox regurgitation into the left ventricle with its concomitant high diastolic pressure was not associated with appreciable dilatation or hypertrophy.

The following notes give a brief account of the microscopical appearance of the parts of which sections were made:

(1) *Ventricle* (left).

Muscle, healthy. Nothing abnormal noted.

(2) *Innominate artery.*

Intima, healthy.

Media, towards inner part of media regularly arranged bundles of plain

muscle circularly disposed and elastic fibres; towards outer part of media, amongst the circularly disposed plain muscle and elastic fibres irregularly arranged groups of plain muscle, many running longitudinally.

(3) *Wall of abnormal coronary artery.*

Endothelium, healthy.

Subendothelial elastic layer, quite well marked. Wall varies in thickness, the thinner parts being at most one-half the thickness of the thicker portions.

Thicker portions: large amount of plain muscle arranged in bundles; rather granular looking elastic tissue between the bundles—apparently split longitudinally in places.

Thinner portions: much less plain muscle than the preceding; towards the centre of one portion of the media, small oval-shaped area which does not stain well: nuclei stain fairly well but are variable in shape. The elastic tissue apparently shows large coarse granules and it appears to become fragmented transversely into more or less elliptical portions.

Externa, well marked.

(4) *Wall of dilated portion of abnormal coronary artery.*

Two layers: (1) External, epicardium;

(2) Internal, part corresponding to wall of the abnormal coronary artery; practically no plain muscle or elastic fibres; rather degenerate-looking connective tissue showing nuclei which stain fairly well, fibrils, and perhaps "ghost-like" elastic fibres.

Interior to the above is a fairly thick endothelial and subendothelial layer showing connective tissue and elastic tissue arranged parallel to the inner surface; nuclei stain well.

Endothelium appears to show proliferation of its cells, the deeper layers of which show signs of organisation.

(5) *Lining of cavity and subjacent myocardium.*

(*a*) Endothelium, normal; no proliferation.

(*b*) Subendothelial elastic layer, fairly well marked.

(*c*) Layer of more or less homogeneous tissue taking up eosin stain, no sign of elastic or muscle fibres.

(*d*) More or less continuous layer of about $\frac{1}{8}$th thickness of (*c*), consisting of heart muscle fibres and white fibrous connective tissue.

(*e*) Vascular layer, thinner than (*d*).

(*f*) Heart muscle proper.

(6) *Junction of dilated end of abnormal coronary artery with ventricle.*

Epicardium and wall of distended portion can be seen separated by heart muscle; the heart muscle ceases and the epicardium and the wall fuse loosely at first, but firmly within a distance of 2 cm. from the point where the heart muscle ceases; epicardium at the point where the heart muscle ceases becomes much thinned quite abruptly, and continues thin for about a distance of

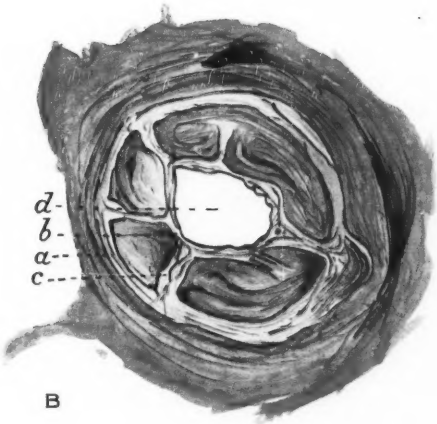


Fig. A. *a*, *a*, *a*, track of abnormal descending branch of the left coronary artery; *b*, cyst-like dilatation at apex.

Fig. B. Wall of dilated part at apex has been opened and held back.

Appearance presented by the pseudo-valvular structure on looking at the apex of the heart: (*a*) external fibrous ring; (*b*) internal fibrous ring; (*c*) radial fibrous band; (*d*) communication between the left ventricle and the abnormal coronary.

REID—Abnormal Left Coronary Artery of Ox Heart

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1·5 cm. as it lies in direct relationship with the wall of the dilated portion; it then becomes thicker, approximating to its original size.

(7) *Branch of abnormal coronary artery.*

Healthy arterial wall.

(8) *Branch of right coronary artery.*

Nothing abnormal to be noted.

(9) *and* (10) *Coronary arteries from normal ox heart.*

Left: the larger vessel; wall of left varies in thickness considerably.

Conclusions in regard to:

I. Course taken by blood during life in the abnormal vessel.

(1) *During systole.* Probably regurgitation occurred from the left ventricle throughout the greater part of systole through the abnormal communication at the apex. This would give rise to a pulse wave apart from the question of the quantity of blood regurgitated. Another pulse wave would be sent along the abnormal vessel from the aorta. In this way the abnormal vessel would be subjected to strain, and the cyst-like part would be subjected probably to the greatest strain. The movement of blood in the abnormal vessel would perhaps be from the apex of the left ventricle towards the aorta.

(2) *During diastole.* The blood-flow in the abnormal vessel would in all likelihood be from the aorta to the left ventricle. The diastolic pressure in the left ventricle and in the abnormal coronary would be high, viz. aortic pressure. Hence conditions would be favourable for increased strain on the abnormal vessel and dilated part during diastole and on the dilated part more particularly during diastole. On the whole, there would be a relative stagnation of blood in the abnormal vessel.

II. Respective proportions of the abnormality, congenital and acquired.

It would appear clear that the communication between the left ventricle and the coronary was developmental wholly. The pseudo-valvular structure must have been present before birth as a congenital peculiarity.

That the abnormal coronary and dilated portion were subjected to abnormal pressures and in consequence became expanded is concluded from the following:

(1) Varying thickness of the wall of the abnormal coronary and dilated part.

(2) The wall does not show the typical structure of a normal artery.

(3) Irregular arrangement of bundles of unstriped muscle etc. in wall.

(4) Evidence of impaired nutrition of portions of the wall of the abnormal vessel.

(5) High diastolic pressure.

In all probability, had the animal not been killed, it would have died at some period of rupture into the pericardial sac through one of the thinned portions of the wall of the dilated portion at the apex.

I am indebted to Professor J. A. MacWilliam for his help and permission to publish the above, and to Mr George C. Kelly for the sketches.

THE EARLY FORMATIONS OF THE MIDDLE EAR AND EUSTACHIAN TUBE: A CRITICISM

By J. ERNEST FRAZER, F.R.C.S. (Eng.),
St Mary's Hospital, Professor in the University of London

Hüschke, to whom we owe the description of the auditory vesicle as a structure derived from the surface layer, was also the first to refer the origin of the tube and tympanum to the mandibular cleft or groove. This view, advanced in 1827 and subsequently, met with very general acceptance by anatomists of the time, and has been more or less prominent since then. It is true that certain doubters have arisen at intervals who denied its truth, altogether or in part: for example, Hunt (1876) working on the pig, came to the conclusion that the region arises from an "invagination" of the pharyngeal mucous membrane, and Urbantschitch (1877) also held that the tube and tympanum were formed by lateral outgrowth which had nothing to do with the first groove, while Kölliker and Moldenhauer (1877) do not appear to have looked on the parts as directly derived from the cleft by modification, but rather from an outgrowth associated with it. Piersol (1888) and Siebenmann (1894) also, with a few others, had views which were not quite in line with the accepted one. However, in spite of defections, the formation of the tubo-tympanic cavity from the first pharyngeal groove has generally retained its hold on anatomists as the orthodox description, and, since 1902, the detailed account on these lines given by Hammar (*Archiv. f. mikr. Anat.* v, 59) has been taken as the standard on which descriptions are based and to which references are made in the text-books and other works dealing with the matter.

In 1910 I first described these parts (*B.M.J.*) as made from the "tubo-tympanic recess" of the pharynx, a recess which has its floor formed by the first two visceral arches, while the third arch makes its posterior boundary. A few years later I gave (*J.A.P.* vol. xlviii) a fuller description, with special reconstructions, etc., amplifying the former more general one. As this description has been adopted in some of our principal text-books, and as it differs in certain fundamental conceptions from the more widely held views of Hammar, it seems necessary to point out[1] where, in my opinion, the earlier representation is open to criticism.

It will be well to confine ourselves, in this matter, practically to the fundamental differences between the two views, and so to avoid a lengthy consideration. The view which I advocate is, shortly, that the tubo-tympanic recess

[1] This was written in 1915. The paper was never finished, however, owing to war work. I have not finished it, as I intended, by some comparative observations, but have confined myself simply to the difference of view in human development.

is a part of the pharyngeal cavity, situated as already indicated, and that it is nearly completely separated from the main cavity by a forward growth derived from the *third* arch, which comes into contact finally with the first arch in the front wall of the recess, so that only a narrow tubal passage is left above the place where they meet. This closing in of the recess from behind only affects its inner part, the outer portion still remaining as the tympanum, thus only communicating with the pharynx by the narrow unclosed front or tubal part of the recess; the tympanum, coming into existence in this way, has in its floor the outer end of the second arch and its groove, in front of this the first groove and arch, while its inner wall is necessarily made by the forward growth from the third arch. Detailed descriptions and accounts of the models can be found in my earlier papers.

There is no essential difference between the two descriptions so far as concerns the separation of the tympanic region from the pharynx by a forward growth, but the origin of this forward growth is referred by Hammar to the *second* arch, and here comes in the fundamental difference. His account of necessity carries the second pouch backwards and inwards, and leaves it on the pharyngeal side of the forward growth, whereas mine leaves it undisturbed in the tympanum, because the forward growth arises on its aboral side. This brief account of the main questions at issue will serve to show the limits of the criticisms I desire to bring forward, and to indicate at the same time the inter-relations of the points with which we are dealing. I propose to show (*a*) that the conditions necessary for Hammar's conception do not in fact exist, (*b*) that those requisite for the view I advocate are present, and (*c*) that the conditions actually found in sections are consonant with and only explicable by the explanation I adduce, and in themselves disprove the other description.

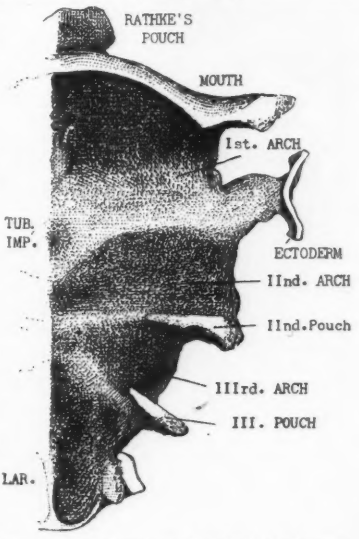

Fig. 1. Ventral surface of left half of pharynx, 7 mm. Shows early stage of recess, with 2nd arch completely in floor. Ectoderm left in contact with 1st pouch; on other pouches the extent of contact with ectoderm is shown by lighter areas.

(*a*) If Professor Hammar's view is correct, and the tympanum is separated from the general cavity of the pharynx by tissues derived from the second arch growing forward between the two, it would seem evident that we ought to find indications of that growth and of its effect on the neighbouring structures. The arch is placed below the floor of the recess (figs. 1 and 2) immediately in front of its posterior external angle, which is made by the dorsal portion of the 2nd lateral pouch.

If the arch thicken, its area as represented in the floor must increase, for if it is going to affect the cavity by enlargement, this enlargement must be in close relation to the cavity. But it does not enlarge: on the contrary, its area becomes smaller, and no condensation is visible within it. Its skeletal bar is close to the lining membrane of the floor of the recess when it first becomes recognisable, and it retains this situation throughout, *except when and where the mass of the forward growth comes in between it and the floor.* It

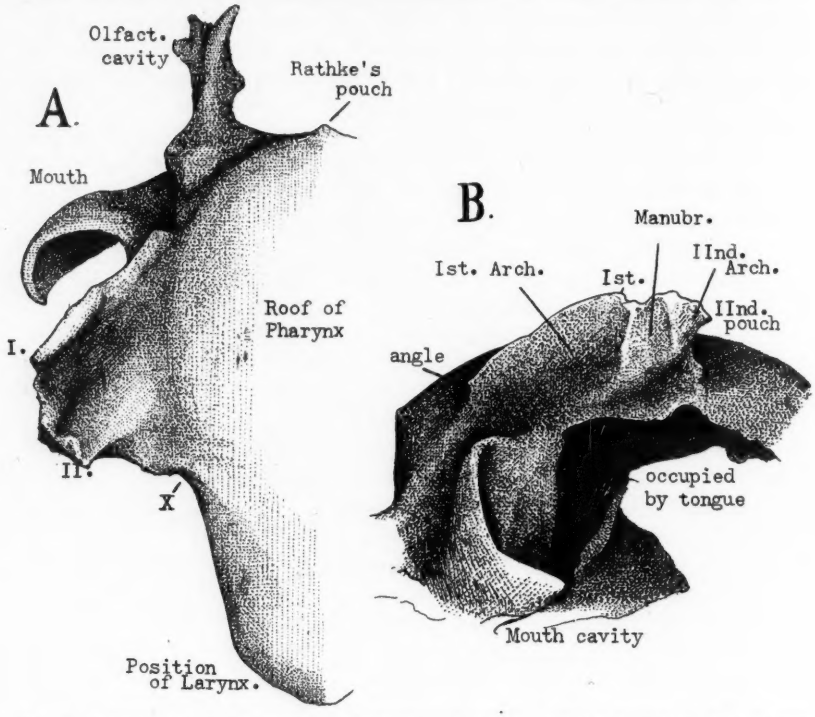

Fig. 2. Pharynx, 16 mm. *A*, dorsal aspect of recess; *I* and *II*, 1st and 2nd pouches; *B*, view from outside, below, and behind, showing area of manubrial invasion, uninvaded remnant of 2nd arch, 2nd pouch, and, internal to these, the impression of the forward growth.

might be said that here we have the enlargement for which we are looking, the evidence of the existence of the postulated growth from the 2nd arch. Certainly it is evidence of growth, but not necessarily from the 2nd arch, and certainly not capable of effecting the results claimed for it: leaving the question of its apparent origin out of the argument for the moment, to be dealt with later, it will be found not to fulfil the conditions that are required if it is to be accepted as the desired effective growth from the 2nd arch. For one of these conditions is that it must be effective from the outer and front

side of the pouch, in the neighbourhood of the outer margin of the recess, not from its posterior margin. But this growth, separating Reichert's bar in part from the floor of the recess, only does so under the inner part of that floor, altogether internal to the region of the pouch, and up to the time of completion of the "separation stage" it does not extend appreciably under the outer part of the floor (see fig. 5). Moreover, there is never at any time any sign of growth in the outer or juxta-marginal part of the 2nd arch, or antero-external to the pouch: the bar remains in contact with the floor here as in the earlier stages, and in fact is there still in the adult as the tympano-hyal. There cannot, therefore, be any question of growth in this part of the arch, unless Reichert's bar takes part in it, on its crest, so to speak. It is hardly necessary to say

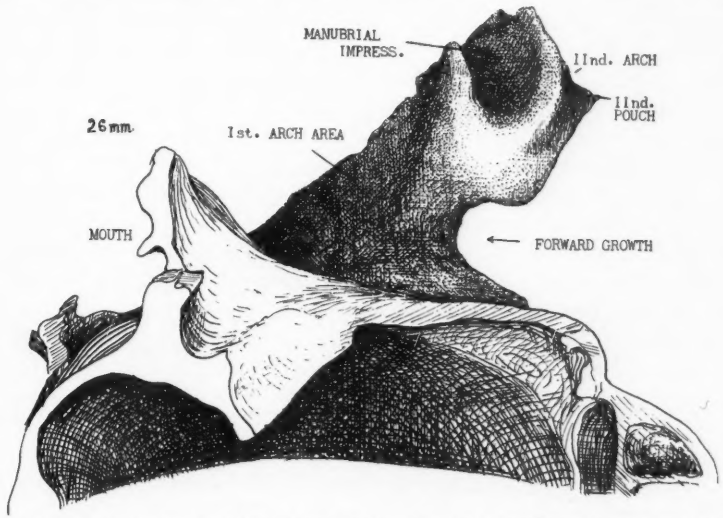

Fig. 3. Pharynx during 8th week from below. To show how the forward growth progresses internal to the 2nd arch area and pouch, next the pharyngeal wall, and is evidently pushing forward from behind.

that the bar has nothing to do with the growth, save that this comes in between it and the more internal part of the recess.

I have given drawings in previous papers illustrating the stages of the growth, and I need only now refer to fig. 2 as showing its definite position. The first view is of the recess in a 16 mm. embryo, seen from above: *B* shows the recess laterally from below and slightly from behind. The triangular area labelled as 2nd arch is the part related to Reichert's bar, but the bar is separated from the recess, further in, by the forward growth, which therefore shows in the model as a hollow between the arch area and the pharynx. This impression shows the growth to be wedge-like, with its base behind. Plainly, it does not affect the outer part of the 2nd arch, and cannot displace the

pouch towards the pharynx, and these characteristics remain. In fig. 3, they are as apparent in the 8th week, though by this time the alleged shifting inwards of the pouch ought to have been accomplished and done with long before. We can say, then, that on the one hand there is no growth capable of causing inward displacement of the pouch, and on the other the growth that is present is not only unable to bring about this movement, but, owing to its situation, could only move the pouch outwards—if it were near enough to affect it at all.

When we come to consider the effects of the postulated growth from the 2nd arch we find a similar absence of evidence that effects which would of necessity result from such growth have any existence whatever in fact. A growth of this sort, if it pushes the second pouch medially must do so by pushing it in front of the structures of the third arch, and must then occupy the place, so to speak, of the displaced pouch, and lie between the structures of the 3rd arch and the lining membrane of the tympanic cavity. These seem to be absolutely necessary consequences of such a process, if it occurs, and afford objective tests to which observation can be directed in the embryo.

In this connection the 9th nerve gives us an excellent standard of position in the various stages. The nerve is a particularly useful 3rd arch structure, for it is placed, from the earliest stages of the recess, immediately aboral to the 2nd pouch, being in fact separated by this pouch from the nerve and bar of the 2nd arch. I have illustrated these relations frequently, and they are indicated in some of the outlines given in fig. 4.

Now it can be said at once that nothing, during the formation of the tympanum out of the recess, passes in front of this nerve or separates it from the lining membrane of the cavity, nor does the second pouch change its relation to it, but continues to project in all stages between it and the facial nerve and bar. The later stages shown in figs. 3 and 4 exemplify this, and these conditions and relations between the parts remain until modified in certain minor respects by developments associated with the later growth of the auditory capsule—but this is long after the separation of the tympanum has been effected and completed. The forward growth begins internal to the 9th nerve, that is, on its aboral side, and is plainly evident a considerable time before the period when the 2nd pouch is displaced according to Hammar's description; it can be seen, already definite, in the 16 mm. embryo shown in fig. 2. At this time, then, the growth is altogether internal to the position of the 2nd pouch, situated between it and the pharyngeal wall, and it increases in size in this situation: yet, if we accept the description given by Hammar, the growth which can be seen to be wedging itself in, from behind, between the pharyngeal wall and the pouch, must suddenly and rapidly displace this pouch inwards, that is, it must begin to press on it from its outer side, and push it inwards in despite of the wedge-like mass which has been laboriously forming itself internal to it. Not only is such a reading of the facts almost impossible in itself, but is absolutely negatived by the observations which

can be made on any human embryos of the proper stages: the inner wedge is a verifiable reality, the positions of the nerves and the pouch are evident, and evidently constant, but there is not the slightest hint of any lateral or antero-lateral pressure on the pouch, or of any shifting of it in front of the 9th nerve, or of any separation of this nerve from its relation to the tympanic cavity by a lateral or antero-lateral growth or in any way whatever. I have given figures showing their relations and conditions in previous papers, where they can be seen if desired, but fig. 4 gives a series of small outlines of some

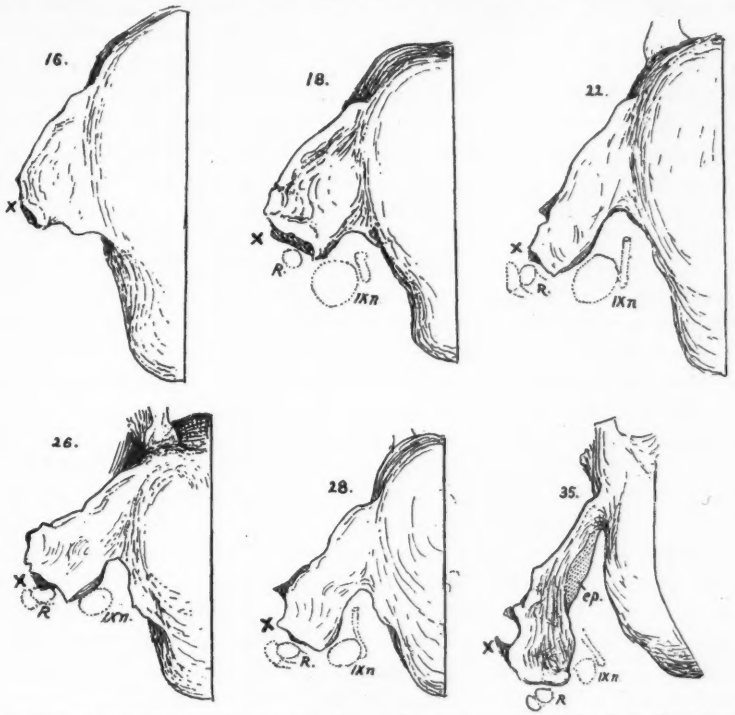

Fig. 4. Dorsal views of stages of separation of recess from pharynx from behind. Embryo lengths are given above each outline. *R*, Reichert's bar; *X*, posterior limit of manubrial invasion; *ep.* epithelial lamina below tubal part.

of the models I have made of this region, and in those in which the nerves are indicated it can be seen that their essential positions with regard to the cavity and second pouch remain unchanged, as does the pouch itself, placed between them.

It is to be regretted that Professor Hammar did not include among his figures illustrations of the ventral aspect of the various stages which he modelled. I confess that I find his accounts of these aspects difficult to follow, but I suppose that his models were very much the same as mine of similar stages,

and for this reason regret the omission of figures, for the ventral aspect is a very interesting and suggestive one where the position and extension of the forward growth are concerned. The floor of the recess, seen from within, such as I have described and figured in this journal (1913), gives a demonstration of these matters perhaps even more striking, at any rate to the observer who is not accustomed to dealing with models of cavities.

We come now to what is, if I am not mistaken, the only direct evidence brought forward in support of Professor Hammar's contention that the 2nd pouch is displaced inwards to the pharyngeal wall. It is the description given by him of the conditions in an embryo of 18·5 mm. (N.S.) length, with an illustration of the model: the drawing is reproduced in Keibel and Mall (text-book) where it can be seen by those who cannot consult the original monograph.

The measurements given by Hammar cannot be compared directly with those given in the references to my specimens, for he uses N.S. length, whereas mine are given in greatest total length. I imagine that his 18 mm. stage would correspond more or less with a "greatest length" of about 22 mm.

I may confess at once that the figure is to me the illustration of some condition quite abnormal: one may make guesses about the nature of the abnormality, but I have no doubt in my own mind as to its existence. I have examined every embryo which I could find sectioned, between 18 and 30 mm., and have found nothing whatever to suggest a remote resemblance to the curious appearance presented by this specimen. This merely negative evidence would not, of course, be of very much weight in itself, and I would have had very great hesitation in stating my belief—however strongly I might hold it —that the specimen is not normal, if that belief did not receive such strong indirect support from these negative observations. For all my specimens exhibit conditions pointing to an even progress of events, such as is illustrated in the series in fig. 4, and among these specimens are embryos of 18, 22, and 25 mm. (not to mention one or two others apparently lying between these limits but of doubtful official measurement). Now these three embryos are all in the line of even progress, as are the 26 mm. and 28 mm., and none show any sign whatever of growth lateral to the 2nd pouch, or of displacement of this pouch: yet somewhere between these stages there is said to occur one in which these things take place, one which therefore starts *de novo*, runs its course, produces its effect, and leaves no sign of its occurrence behind it, and all this while the embryo is increasing in length some 2 or 3 mm. The mere statement of the necessities that follow on the negative observations to which I have referred is enough to indicate the support they render to the opinion formed on the first view of the figure of the model, and, when the existence is remembered of the solid forward growth internal to the pouch, the suggested occurrence would seem impossible. I do not wish to lay stress on the appearance of the "pouch" in this figure, though it is strangely incompatible with the idea of a structure being possibly displaced by solid growth, and I am

content to leave the matter here, pending an explanation of the curious condition which will enable it to occupy its proper place.

The argument, then, against the acceptance of the explanation given of this 18·5 mm. (N.S.) specimen is not founded on its extraordinary appearance, but on the stability of relations between the pouch and the structures on each side of it, and the wall of the recess close to them, and on the impossibility of conceiving the necessary growth appearing and acting and disappearing in the very short intervals existing between the specimens examined. The argument, to my mind, is an effective one, and disposes of any attempt to shift the pouch across to the pharynx, whatever may be the opinion held about the specimen concerned.

This, of course, does not necessarily affect the fact that a remnant of the 2nd pouch is found on the pharyngeal wall. It is more convenient to deal with this later: for the present it is enough to point out that the remnant is there long before the postulated "shifting" is said to occur, so that the theoretical necessity for supposing such a movement as that which we have just been considering does not exist.

(*b*) Turning to the consideration of the view which I advocate, it is evident that a good deal of what has been said already is applicable positively in its favour. Thus, the forward growth takes place from behind, on the inner or aboral side of the 2nd pouch, i.e. from the area of the 3rd arch: the 2nd pouch remains unaffected, altogether external to, and on the oral side of, the growth: the growing mass pushes the limits of the recess-cavity before it, hence must pass forward over the 2nd arch structures, and so we find it separating the skeletal bar from the recess: but the outer part of the bar still remains in relation with the outer part of the floor of the recess, which becomes a postero-external part of the floor (outer wall) of the tympanum as the separation proceeds. It is unnecessary to dilate further on these matters, for their bearing on the question is quite clear, and I do not think there is any fact whatever, either of direct observation, or of any "necessary effect," which is not in absolute accordance with the view which I have brought forward concerning the nature of the forward growth. As for the particulars, they can be considered with the following section.

(*c*) *The conditions in the human embryo.* I have previously given full accounts, with figures from models, etc., of the various stages of evolution of the tube and tympanum from the tubo-tympanic recess, so that it is only necessary here to run over the main facts of the stages. In fig. 4 are given miniature reproductions of the outlines of the region concerned as found in the models made from various stages: the series is not complete, but it is unnecessary to put others between those shown. The most important difference between the early and late members of this series is plainly that due to the increasing concavity of the posterior margin of the projection of the tubo-tympanic recess: this margin proceeds at first with an irregular line inwards and rather backwards from the 2nd pouch to the pharyngeal wall. There

quickly comes a forward bowing of the line, growing into a marked and deep forward convexity, particularly noticeable towards the inner part of the margin, and this progresses until only a constricted tubal portion is left connecting the pharynx and the tympanum. This concavity is produced by the forward growth which we have been discussing. The area of the second arch is seen on the lower aspect at 7 mm. in fig. 1. It is invaded later from in front by a manubrial extension from the 1st arch, and only a small portion of its territory remains uninvaded, namely the posterior part, covering Reichert's bar and just in front of the 2nd pouch. The 2nd pouch can be seen from the dorsal side as an angular projection in all the stages shown in fig. 4. The manubrial invasion, the position of which within the area of the 2nd arch is described by Hammar, is marked behind by the little secondary point *X* in the outlines, so that the remaining unchanged part of the 2nd arch is easily placed between this and the blunt angle of the 2nd pouch.

If we come now to consider the genesis of the forward growth which determines the general arrangement of the regions, it would seem clear that it can only be one of two things. The shape of a cavity, such as that of the pharynx or the tubo-tympanic recess, depends on the structures that form its walls, and we cannot imagine that the cavity itself, or its lining layer, possesses the power to alter its form: power of growth exists, of course, in certain parts, as in the lateral pouches, but it cannot be claimed for the layer in general, and even in the case of the pouches the direction in which the growth is effective seems to be determined by the surrounding structures. The only structures in relation with the floor of the recess, and determining its form, are the mesodermal pharyngeal arches, and the cavity lies compressed between these and the otic capsule, etc., in relation with its roof. The forward growth begins in the floor region, as can be seen in fig. 2, and hence has an "arch value" in origin, and, as it evidently appears near the hinder part of the recess, the 1st arch can be excluded. The floor growth, as can be seen in figs. 2 and 3, and especially in reconstructions of the recess seen from within, such as I have shown in vol. XLVIII of this journal, is evidently pushing forward from the region of the back wall of the recess, and as it increases in size it begins to push this back wall forward and thus to cause the concavity here as seen in "cast" models, so that the floor growth is a little in advance of the concavity. But the hinder wall of the recess is from the beginning made by the 3rd arch, so that the forward growth must be looked on as derived from this arch, and all its relations and details seem to be consonant with this origin. Some of these have been brought forward earlier in this paper, and others have been dealt with at greater length in previous papers: I need not recapitulate these nor I think lay any further stress on the matter, for it seems to me almost self-evident, and apparent to any unprejudiced eye looking at the reconstructions.

The outer part of the 2nd arch remains undisturbed, with its pouch angle, though the whole region is pivoted round a little so as to face somewhat

differently, but the rest of the arch is separated from the floor of the cavity by the increasing thickness of the forward growth. This can be well seen and appreciated in the reconstructions of the floor (1913) but are shown here (fig. 5) in another way: the drawings are from linear reconstructions made along the line of the hyoid bar, showing its relations with the floor, and exhibit the increasing thickness and results of the new growth passing between the bar and the floor of the recess. Different enlargements are used, to make the sections more or less of the same size. The line of section is not transverse, but would meet its fellow of the opposite side at a wide angle, being directed

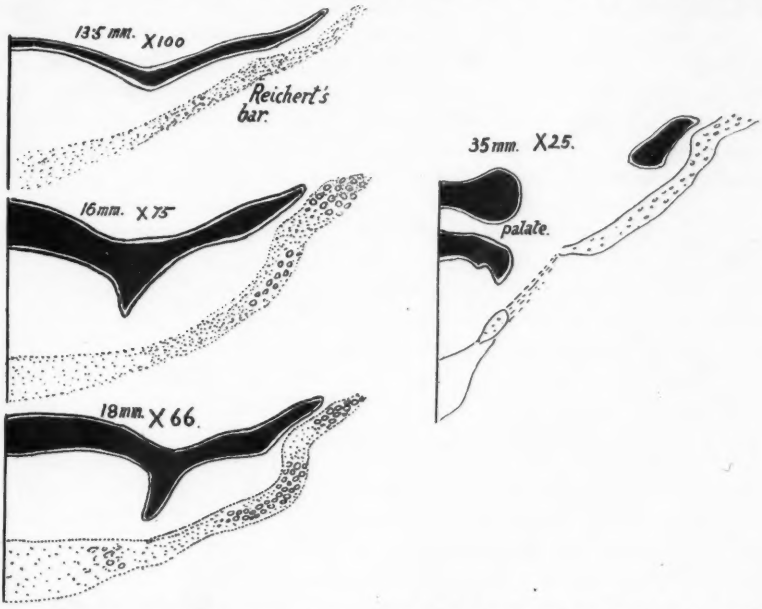

Fig. 5. Reconstruction sections across pharynx in the line of Reichert's bar. To show increasing distance between bar and inner part of recess due to forward growth. Outer part of bar remains in relation with recess.

rather forward, so that the breaking of continuity between tympanum and pharynx from behind does not appear in the sections till relatively late. The first sections show the increasing depth of the growth, and sinking of the hyoid bar, correlated with increasing height of the pharyngeal cavity (of which the growth is seen to form the outer wall here) while the general level of the recess and of its pharyngeal opening is kept at about its original position with relation to the roof of the pharynx. This relation of the growth from the 3rd arch to the pharyngeal wall gives it the opportunity of sending a process forward to join the (maxillary) palate fold, which process then becomes apparent on the pharyngeal wall as the pharyngeal extension of the palate. I described this

process first in 1910; subsequently Michio Inouyé showed the pharyngeal extension to be a secondary part, joining after its appearance, in moles and mice.

Reconstructions in this line of section through the second month exhibit little additional (save that the palate extension begins to show) and are not reproduced, but at 35 mm. the growth has definitely pushed the hinder border of the recess over the line of the bar: here the survival of the relation between bar and recess is seen in the outer part, while the hinder part of palate fold, which has elongated, comes into the section and illustrates its association with the growth.

The 2nd pouch, the angle seen between the 9th nerve and the nerve and bar of the 2nd arch, remains throughout the series. Hammar, believing that this pouch—which he recognises as such in his earlier specimens—undergoes shifting in his 18·5 mm. (N.S.) stage, naturally does not recognise it in the recess after this: but his reconstructions of later stages show it nevertheless, although it has not been dignified by labelling. I need not repeat what I have said already about the constancy of its relations, but I desire to insist on these as matters of primary importance, for *the pouch cannot move when the structures in front of it and behind it are undisturbed, and when nothing comes between them and the lining of the cavity in relation with them.* Whether the angle is really the dorsal part of the pouch or merely the stump of this part is only of academic interest, but the constancy of relations is practically the important matter, and is enough to ensure that the angle in the later stages is the same thing as that in the earlier ones, with all the consequences which I have endeavoured to show depending on this.

Two more points remain for consideration. The first has to do with the existence of a derivative of the 2nd pouch on the pharyngeal wall, claimed by Hammar to be the displaced structure originally found on the recess. I have never wished to deny the pouch-value of this, for I believe it to be a part of the 2nd pouch, but only to represent its ventral portion: the dorsal portion remains as the angle so frequently mentioned, and the forward growth passes forward between the two. The elongated pouch of a 7 mm. embryo is seen in fig. 1. As the head grows in breadth the outer and dorsal part is drawn out still further, and contact with ectoderm (precervical sinus) becomes confined to the inner part. An embryo of 13·5 mm. shows the drawn out pouch extending along the lower aspect of the short hinder margin of the recess, and from its inner end, definitely on the pharyngeal wall, there is the remnant of the external pharyngeal duct leading down towards the former site of the precervical sinus. A 15 mm. embryo shows the complete pouch, though much less clearly, and even at 16 mm. (fig. 2) there appear to be remnants of it in the irregularities on the posterior margin of the recess: but although the forward growth is breaking up this intermediate part of the pouch, its outer and inner (dorsal and ventral) portions remain unaffected, on the recess and side wall of the pharynx respectively. This short account will show that I differ

from Hammar in that I recognise this pouch-remnant as being there *ab initio*, and it can be found there by anyone who takes the trouble to look for it.

The second point does not directly concern the main object of this paper, but I call attention to it because of its possible bearing on the explanation of certain cysts found immediately below the petrous region—cysts which are put into that heterogeneous collection which clinicians lump together as "branchial," but which certainly are not branchial if that term were used in its proper sense. The point referred to is the occurrence in the normal development, in the last phases of the "separation stage," of an epithelial (double) lamina below the short tubal connection between tympanum and pharynx.

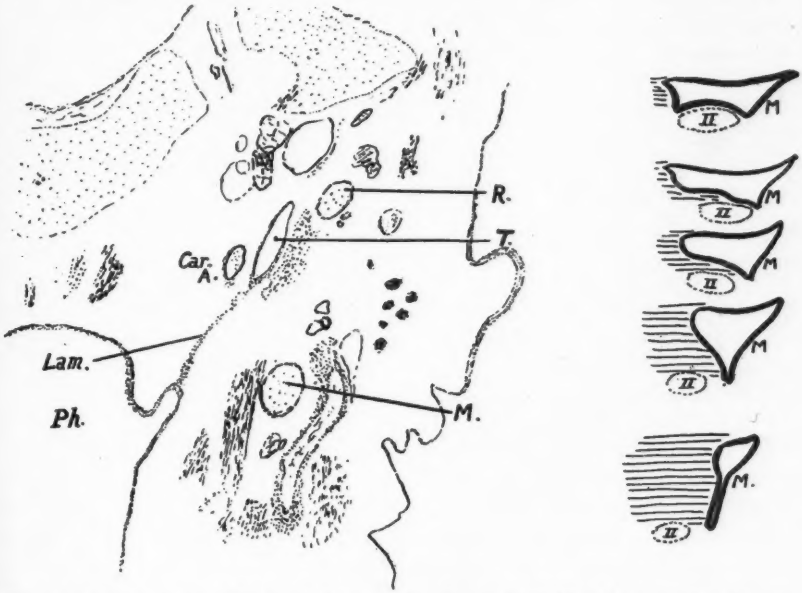

Fig. 6. (*a*) Section, 35 mm. below level of patent tube. *Lam.* epithelial lamina connecting pharynx (*Ph.*) with tympanum (*T*); *M.* Meckel's cartilage; *R.* Reichert's cartilage.
(*b*) Schemes to show formation of lamina; explanation in text.

Its extent is seen in the 35 mm. reconstruction in fig. 4 and its appearance on section is shown, with diagrams representing its formation, in fig. 6. The first of these diagrams is a scheme of a section across the inner part of the short recess of an early stage, parallel with the wall of the pharynx: the 3rd arch (horizontal lines) forms the hinder part of the floor and limit of the recess, the 1st arch (*M*) forms its front part, and the 2nd arch (dotted area) is between these two in the floor, separated from them by the 2nd and 1st grooves respectively. In the succeeding schemes the 3rd arch is seen to extend forward under the lining membrane, over the second, obliterating the 2nd

groove in doing so, and gradually pushing in the hinder boundary of this part of the recess. The 2nd arch thus drops out of relation with the recess here.

The forward growth of the 3rd arch goes on, pushing in the back wall still further, but along the floor it is limited in front by the first groove. The result is that the growth applies itself to the surface of the 1st arch; the lower portions of the epithelium, thus pressed together, adhere, and so the epithelial lamina is formed. The tracing of a section from a 35 mm. embryo exhibits this lamina connected on the one hand with the lining membrane of the lower part of the tympanum, and on the other with the lower part of the pharyngeal opening of the tubal part, through both of which parts the section passes.

It is clearly evident that the original 1st groove is represented by the free edge of this lamina (see schemes) and has nothing to do with the formation of the cavity of the tube, which is really a remnant of the old recess cavity, persisting in its most anterior part, immediately below the roof. The tube is more or less parallel with the groove, although this is not quite a true description, but the common statement that it *is* this groove is wrong and misleading in many ways, and ought not to be made by anyone acquainted with the details of its ontogenetic development.

The epithelial lamina, made in this way, does not seem to last very long. It is well marked in my specimens of 35 and 37 mm., it is apparently commencing in a third of ? 32 mm., and there is no sign of it in one of 40 to 42 mm. It seems to be at its best about the 35 or 36 mm. stage. I have not, so far, found any apparent remnants of it in still older specimens, but the possibility of such remnants existing is undeniable and for this reason—as well as from a desire to foster a truer conception of the formation of the tube—I call attention once more to its presence.

This paper has been almost entirely controversial, and hence difficult to summarise. I have endeavoured in it to show that the conditions which *must* be present, if Hammar's description is correct, do not in fact exist; that those which must be present if my description is accurate are in fact there, and the description is founded on them; and that the stages found in the human embryo are only consonant with the explanation I have given of them. This means that the separation of the tympanum from the pharynx is effected by a forward growth from the *third* arch, and not from the *second*, as Hammar maintains, and that the outer part of the 2nd arch, with the dorsal part of its pouch, remains in the tympanum. The ventral part of this pouch is on the pharyngeal wall.

I have also recalled the existence of an epithelial lamina below the developing tube, and have pointed out that the tube cannot be described correctly as a persisting first pharyngeal groove.

THE DESCRIPTION OF A NEANDERTHALOID AUSTRALIAN SKULL, WITH REMARKS ON THE PRODUCTION OF THE FACIAL CHARACTERISTICS OF AUSTRALIAN SKULLS IN GENERAL

By A. St N. BURKITT, B.Sc., M.B.
AND
J. I. HUNTER, M.B., Ch.M.
From the Department of Anatomy, University of Sydney

The skull which is the chief subject of the following description belongs to the incomplete skeleton of an Australian aboriginal presented by J. R. Glyde, Esq., of Sydney, New South Wales, to the Department of Anatomy, University of Sydney. The skeleton had been exhumed at Tamworth in 1880, and was known to be the remains of "Jenny" an aboriginal female.

The skull exhibits an enormous development of the superciliary ridges and glabella, a comparatively well developed bregmatic eminence and a marked development of the torus occipitalis. Added to these primitive features are an extremely low sloping forehead, and a forward slope of the occipital plane of the os occipitale, so that the maximum occipital point coincides with the inion. These features have been referred to in this place on account of the presence of similar characteristics in Neanderthal skulls, a fact which prompted the present description. In addition the aboriginal crania in the Australian Museum, Sydney, and in the University of Sydney Medical School Collections (1. Museum of Normal and Morbid Anatomy, and 2. Anatomy Department) have been investigated for the purposes of comparison. The general results of this survey are embodied in this paper.

The skull which is specially described in this paper will be referred to under its catalogue number (No. 792, Anatomy Dept. Collection). Where special features of other skulls of this collection are recorded, such skulls are indicated by plain catalogue numbers. Skulls selected from the Museum of Normal and Morbid Anatomy (Medical School) are specially indicated. The Australian Museum skulls include the Roth collection, comprising 90 specimens, which were described by Klaatsch (12). We wish to acknowledge our indebtedness to Klaatsch's work. We have followed his plan of description and tables of measurements of Australian and pre-historic skulls, as a basis of comparison. The Western Australian Skull (B. 10283 Australian Museum) and the South Australian (No. 1719 Stuttgart Museum) referred to in this paper were also described by Klaatsch. When specimens of the Roth series are referred to they will be indicated by their original Roth number. The remaining skulls of the Australian Museum collection are indicated by their catalogue number.

I. Facial Skeleton

(*a*) ***Supraorbital, Nasal and Orbital regions.*** The glabella and superciliary ridges of No. 792, which are of coarse texture, reach a degree of development which exceeds that of any other modern skull examined by us. This great development of the superciliary ridges together with an exceedingly low sloping forehead, are the two factors which determine the primitive appearance of the forehead as seen in Pithecanthropus and in the Neanderthal specimens

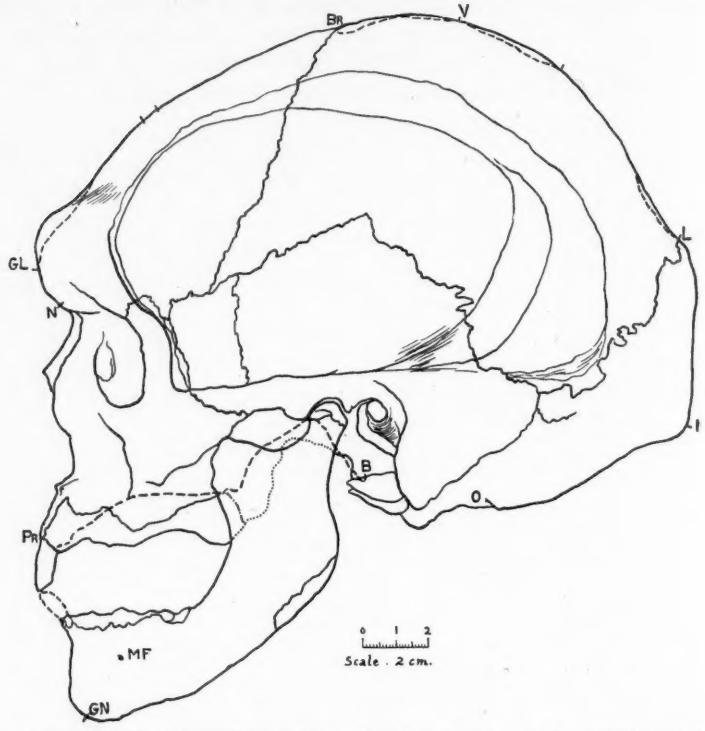

Fig. 1. Norma lateralis of Australian skull (No. 792) (Frankfurt plane). The dotted line indicates the median plane of the skull.

(fig. 1). The projection of the glabella in front of the most depressed portion of the bridge of the nose is 16 mm. This has been measured by making horizontal sections of the skulls with the aid of Lissauer's diagraph (fig. 4). The medial angular process is also well marked, exceeding that of the Kalkadun skull (R. 62), a specimen which Klaatsch remarked upon as presenting an excellent state of development rarely so pronounced amongst Australian aboriginals. The vertical height of the superciliary ridges in the region of the supraorbital notch in the Kalkadun skull is 13 mm. whereas in No. 792 this

vertical diameter is 18 mm. (right) and 21 mm. (left). Laterally the vertical extent and prominence of the ridges decrease, but in the region of the external angular process there is an increase in the size of the ridges forming a massive lateral projection. There is therefore present a torus supraorbitalis corresponding to Type III of Cunningham (5) and resembling that present in the Neanderthal specimen. There is a pronounced depression between the supraorbital ridges as they pass inferiorly to fuse with the glabella—an additional Neanderthal feature. In No. 792 the distance of the deepest point of this depression (facies supraglabellaris) from the nasion is 29 mm.; a comparison with the distance of this point from the bregma (99 mm.) gives an index of 29·29 (Schwalbe's index) which is within modern limits (21–30). The Neanderthal is considerably higher, 43·1 (Klaatsch) and Spy II, 34·4 (Schwalbe).

The absolute measurement with the tape from nasion to ophryon in No. 792 is, however, 43 mm. as compared with 41 mm. in the skull of an Australian aboriginal in the Turner series (XXIX. B. 12, Cunningham (5)) and 43 mm. in the Neanderthal cranium. The correspondence of No. 792 to the Neanderthal in this respect emphasises the inadequacy of Schwalbe's index, as mentioned by Klaatsch and Cunningham.

The division of the superciliary ridges into a medial "arcus superciliaris" and a lateral "planum supraorbitale" is practically absent in No. 792. This absence is a primitive feature. The absence of this subdivision in No. 792 is more complete than in the Kalkadun skull, another point of resemblance to the Neanderthal specimen. This serves to emphasise the contention of Cunningham and Klaatsch in opposition to Schwalbe, that the subdivided condition of the superciliary ridges in living races is not a point of distinction from Neanderthal types, which can be applied absolutely, for, as in this instance, an Australian skull has occasionally to be excepted.

Above the tori supraorbitales, the facies supraglabellaris passes laterally into the sulci superciliares; these extend to the temporal crests, over which they pass into the temporal fossae. These sulci are not so pronounced as in the Neanderthal calvarium, but apparently approximate to the N.S.W. and Queensland specimens (XXIX. B. 12 and XXIX. A. 10 respectively) figured by Cunningham (5). Though shallow, these sulci attain a width of 15 mm. on each side which is less than in the Neanderthal but greater than in the abovementioned N.S.W. cranium. These sulci look upwards, as well as forwards, a character which obtains to a greater degree in the Neanderthal (fig. 7).

Section of the skull revealed the fact that there was present an unusually large frontal air sinus (fig. 2). Cunningham (5) quotes Logan Turner, who found that by illumination he was able to map out these sinuses only in 20 out of 69 aboriginal skulls, and that it was altogether absent in 30·4 per cent. Relatively small frontal air sinuses close against the inner table of the cranial wall, bounded in front by a thick layer of condensed bone and situated at the base of the torus, are as Cunningham points out, usually to be found in the Australian aboriginal, who in this respect, forms a link with the Neanderthal race and

anthropoids. In No. 792 the condensed outer table of the frontal bone reaches a maximum thickness of 7·5 mm. at the glabella. The sinus on each side extends laterally for 4·3 cm. upwards between the tables of the frontal for 4 cm., and backwards between the two laminae of each orbital plate of the frontal almost to its posterior border. Posteriorly, the inner table of the squama frontalis is only 1–2 mm. in thickness. The maximum interval between the opposed surfaces of the two tables in the mid-line is 18 mm. There is a medial frontal sinus opening into the right infundibulum in addition to the lateral excavations. The extraordinary combination of a large torus and a large

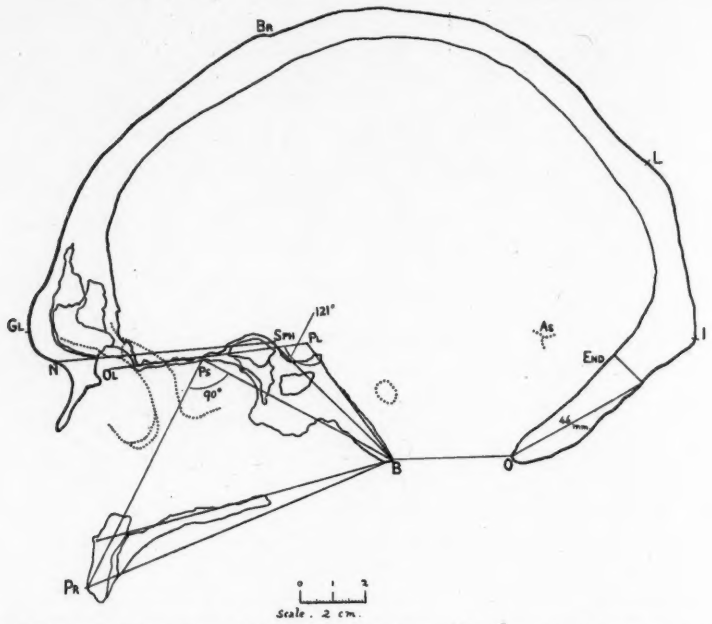

Fig. 2. Median sagittal section of Australian skull (No. 792). The external auditory meatus, the asterion and the margins of the orbit are superposed on dotted outline. *Ol. Pl.* indicates the plane of the cribriform plate.

frontal sinus lead to the result that the supraorbital region of the frontal forms a considerable part of the orbital roof. The greatest length of the precerebral part of the roof of the orbit in the mid-supraorbital region is 25 mm. in No. 792 compared with 20 mm. in the Neanderthal and 16 mm. in the N.S.W. cranium (XXIX. B. 1 Turner series) described by Cunningham (5). In this way the size of the frontal lobe is greatly limited. The combination of large tori supra-orbitales and large frontal air sinuses found in No. 792 is, however, apparently very similar to that described by Cunningham (6) in the head of Boco, an aboriginal from South Australia. In this case the glabella was 30 mm. anterior

to the frontal pole of the cerebral hemisphere, compared with 26 mm. in No. 792.

In many respects the nasal region exhibits typical aborigina features to an average degree. Below the well-marked nasion, there is a second depression which corresponds with the upper margin of the projection of the nose in the living state. The nasal bones together present the usual saddle-shaped appearance. The medial borders of these bones which are partly synostosed, project moderately, showing a tendency to bridge formation, more pronounced than in many Australian skulls. On the other hand, No. 795 presents a well-marked bridge without any sign of a nasal depression. In some cases the nasal bones besides being on the whole small, narrow to such an extent superiorly that the frontal processes of the maxillae are separated by only a narrow interval (4 mm. in No. 620). In R. 87 (aboriginal child) the processes meet superiorly behind the nasals.

The lower margin of the apertura piriformis presents the usual aboriginal features. The anterior nasal spine is poorly developed. There is a well-marked fossa praenasalis on each side below. This is limited anteriorly by a crest ("crista praenasalis"), which is continuous with the lateral sharp boundary of the apertura piriformis. Posteriorly this fossa is bounded by a second crest ("margo infranasalis"), which runs laterally towards the commencement of the inferior concha (fig. 6).

In No. 792 the lower limits of these two crests are indistinct, but in B. 10510 (Australian Museum) they converge towards one another and terminate in the spina nasalis anterior. In this way the "crista praenasalis" forms the inferior boundary of the apertura piriformis, and the fossa praenasalis is situated in the floor of the nasal cavity. In the majority of the Roth skulls the crista praenasalis becomes indistinct above the roots of the incisor teeth. Examples of a distinctly bifid anterior nasal spine are seen in Nos. 2355 and 2356 (Medical School Museum). The spine is prolonged into a median crest between the incisors in No. 477 (Medical School Museum).

The outstanding feature of the nasal region is that the skull falls into the leptorrhine class, the nasal index being 47·2. In his Challenger Report, Turner (19) says that all observers agree on the platyrrhine character of Australian skulls. Some are mesorrhine, but the leptorrhine condition is practically unknown, though Turner's authentic Mudgee skull was of this type. Nevertheless, as shown above, certain features, e.g. the well-marked nasal depression, the depressed nasion above this, the narrow nasal bones, poorly marked bridge and the fossa praenasalis, are typically Australian features.

By Cameron's method (4), the naso-orbito-alveolar index was measured on the projection of the norma facialis and this placed the skull in his group III which includes Australian aboriginal, Negro and Melanesian skulls.

The orbit in No. 792 has a shape intermediate between the large approximately circular type and the vertically compressed type.

The infraorbital fossa is an undivided depression. Of the specimens under review, it is exceeded in depth only in a Queensland skull, B. 10510 (Australian Museum), where there is a remarkable excavation undermining the infra-orbital margin.

That part of the zygomatic bone which enters into the formation of the margin of the orbit is not sharp but has a rounded bevelled border. Turner (19, p. 32) says in regard to this point, "the orbits in the males were characterised both by the massiveness of the upper orbital border and by the peculiar breadth and curvature of the malar bone where it formed the outer boundary, which wanted the sharpness one sees in crania generally." Klaatsch also directs attention to this feature for which he offers no explanation. For the following reasons we believe that the rounded character of the inferior orbital margin is due to the large size and great degree of wearing of the molar teeth often to be found in Australian aboriginals:

Firstly, the rounding of the orbital margin is most marked in those skulls with a marked degree of wearing of the teeth. Klaatsch (12, p. 79) refers to R. 16 as showing a degree of wear corresponding to many pre-historic European skulls, and greater than that of any other aboriginal he had examined. In this skull the orbital margin is exceptionally well rounded. A survey of the collections under consideration, proves that this relationship exists in the majority of cases.

Secondly, the bevelled or rounded condition of this border is not found in childhood and is only slightly present in early adult life in the specimens under review. It is apparently acquired therefore in adult life, following the usage of the permanent dentition.

Thirdly, in those skulls in which the teeth were neither massive nor well-worn, the orbital margin was usually sharp, and the zygomatic bone was not massive (e.g. R. 12, R. 49).

We, therefore, conclude that the amount of use of the molar teeth by a given individual, together with the massiveness of the teeth in the Australian aboriginal, contributes to the formation of a rounded orbital margin. There are exceptions to this, however, a sharp orbital margin sometimes being present, together with well-worn teeth. In these cases the masticatory apparatus was less well developed, the palate being usually narrow and the teeth comparatively small (R. 82).

Features associated with this rounding of the margin, are a broadening of the cheek region and a lateral convexity of the zygomatic arch, as mentioned by Turner. This gives rise to the diamond-shaped appearance of the face often observed in the Australian aboriginal (Cunningham (6)).

We consider also that these features are due in part to the operation of mechanical factors. The zygomatic bone is strengthened in order to accommodate the masticatory muscles and to support the force transmitted upwards by the molar teeth during grinding. So marked is the increase in bone formation in the case of R. 2 that a ridge is formed on the zygomatic

bone. It is directed antero-posteriorly so dividing the outer surface of the zygomatic bone into two portions. The upper of these two surfaces is separated from the orbital cavity by a smooth rolled border (the lateral and inferior margin of the orbit). In this case the massive molars are extensively worn.

The zygomatic arch of No. 792 has an upward convexity, while the roots posteriorly form a plate which bears inferiorly an extension of the glenoid fossa. The thickness of this plate is 6 mm. compared with 9–10 mm. in Spy II.

The lower border is irregular being distinctly notched by an impression for the masseter. There is a lateral convexity, the greatest inter-zygomatic diameter being in the temporal segment; this portion of the arch measures 11 mm. vertically and 5 mm. transversely. The strength of the zygomatic arch in the skull of the Australian aboriginal is to be correlated with the racial features exhibited by the facial skeleton.

The Mechanism of Production of the Facial Characteristics of the Australian Aboriginal.

The zygomatic arch forms a massive support for the masseter muscle while its lateral convexity increases the size of the temporal fossa to accommodate the other muscles of mastication. In addition to accommodating the masticatory muscles, this stout arch forms a buttress of support for the body of the zygomatic bone which receives and transmits the stresses and strains which it receives from the maxilla. Now the teeth of the aboriginal, which are usually massive, have to contend with a molluscan, fibrous and often gritty diet. On account of these factors, the maxilla must be of stouter structure and in consequence a general massiveness results. The molar teeth are mainly supported by the vertical ridge of the maxilla proceeding vertically upwards to the zygomatic process, while the canines and incisors (as in the gorilla) transmit their thrust through the frontal process of this bone. These columns may increase in size to such an extent that the area above the premolars appears hollowed out, i.e., there is formed an infraorbital fossa (R. 2 and R. 24). In other cases this fossa may become deep through an actual excavation. In these cases the roots of the teeth may be divided into two sets as in R. 12. In this specimen the vertical ridge of the maxilla supports the roots of the molar teeth which converge towards it, while the roots of the premolars slope forwards towards the frontal process. When, however, the molar-premolar root arcade is uninterrupted in specimens which exhibit a tendency to squareness of the palate as in R. 10, R. 24, R. 35, R. 39, and R. 69, then the infraorbital fossa is often absent or very shallow. This is because force is transmitted vertically upwards to the infraorbital margin, between the main pillars of support. These features explain why all grades of development of the infraorbital fossa are possible in Australian skulls.

In Australian aboriginals, the frontal process is usually stout and powerful. It supports the thrust of the incisors, canines and sometimes the premolars. The two frontal processes often approximate to one another being separated

only by narrow nasal bones. In many Australian skulls they are supported by a relatively large medial angular process.

The molar teeth are supported by the vertical ridge of the maxilla, which transmits the strains received by it to the zygomatic bone. Thereafter the strain is mainly supported by the fronto-sphenoidal process of this bone. From thence it passes to the external angular process of the frontal. The result of this increase of strain, leads, we believe, to increased bone deposition in the vertical ridge of the maxilla in the zygomatic bone, and in the external angular process of the frontal bone. The fronto-sphenoidal process of the zygomatic bone and the external angular process of the frontal bone, are often markedly tuberculated on this account. This increase of bone formation as already shown also extends to and rounds off the orbital margin.

When a low sloping forehead and a depressed nasion are combined with massive jaws and teeth, as is often the case in the Australian aboriginal, the supraorbital ridges tend to be enormously developed (cf. Thomson (18)). Elevation of the frontal bone accompanied by a decrease of masticatory power, causes a diminution in size of this torus. The diminution first occurs over an area between the strong medial angular process and arcus superciliaris medially and the tuberculated lateral angular process laterally, to each of which, the stresses from the maxilla are directly transmitted; this intermediate area becomes the planum supraorbitale. In this region the elevated frontal bone is sufficient support without the addition of a torus.

The zygomatic arch also serves, through its inferior border, as a rod of resistance against the mandibular force as well as a support for the masseter. These factors again demand that this arch should be stout and strong.

(*b*) *Prognathism.* The general prognathism of the facial region of No. 792 was measured by Fraipont's method on the diagram of the norma lateralis (fig. 1). The line drawn from the glabella at right angles to the glabella-lambda line, passes in this case through the alveolus of the second incisor. Klaatsch found in the specimens of the Roth collection that it passed through the first premolar or more posteriorly; this is in agreement with Fraipont's results. No. 792 shows that the prominence of the glabella so greatly influences the position of this line that, in calvaria in which it is markedly developed, reconstruction of the facial region cannot be carried out on the assumption that the above-mentioned line will pass through the premolar region without allowing for a great margin of error (12–13 mm. in No. 792).

A second line parallel to the vertical line through the glabella and touching the most prominent point of the incisors (approximately determined owing to the teeth being absent), cuts the glabella-lambda line 4 mm. in front of the glabella (see fig. 2). This is considerably below the lowest figure quoted by Klaatsch, viz., 8 mm. in the Kalkadun skull (R. 62). Again, the prognathic angle between lines from prosthion to glabella and prosthion to inion, is 82°. The greater the facial projection the lower is this angle. Klaatsch records it as low as 70° and as high as 81° in the Roth series. Therefore, when measured

by these methods, No. 792 appears to be more orthognathic than any in the Roth series. Flower's gnathic index which is independent of the degree of development of the glabella, places it well within the limit of orthognathic skulls, the index being 95·23. Turner (19) records five orthognathous male specimens and Duckworth (7) found the range in the Cambridge Collection to be 93·4 to 108·7 in males and 95 to 108·7 in females.

Though apparently No. 792 is orthognathic, there is a decided tendency to alveolar prognathism. A measure of this was obtained by recording the angle between the following lines: (1) The line of the alveolar margin in the norma lateralis, and (2) The line from the naso-spinale to the prosthion. The angle proved to be 68°. The greater the projection of the alveolar process the smaller will this angle become.

For purposes of comparison, we have measured this angle in Klaatsch's selected specimens from the Roth series and the following results were obtained shown side by side with the figures obtained by Fraipont's method and by measuring the glabella-prosthion-inion angle:

	Distance on glabella-lambda line (Fraipont)	Glabella-prosthion inion-angle	Angle of alveolar prognathism of maxilla
R. 2	25 mm.	70°	64°
R. 12	11	80	62
R. 16	22	70	62
R. 24	20	72	55
R. 28	19	72	67
R 57	24	70	56
R. 60	19	74	50
R. 62	8	81	68
R. 80	12	71	60
Stuttgart 1719	24	69	64
B. 10283 (W.A., Sydney Museum)	23	70	44
London Collection, S. 1406 ...	23	73	45
No. 792	4	82	65
European (Australian Museum)	8	76	73

This table at once shows that No. 792, though orthognathic, has definite alveolar prognathism. It also shows the three types of prognathism which are possible. There may be combined (1) an alveolar projection with a general facial prognathism (R. 2, R. 24, R. 57, R. 60, B. 10283, N. 1406, R. Coll. of Surgeons), (2) an alveolar projection without a general prognathism as in No. 792, R. 80, R. 12, (3) absence of facial prognathism and also of any marked degree of alveolar projection (R. 62, European).

R. 80 and R. 12 also show that the ape-like horizontal condition of the sub-nasal region found in aboriginals is not necessarily associated with general facial prognathism, so that orthognathic skulls may thus preserve this primitive sub-nasal projection (cf. Topinard (19, 23)).

A sagittal section of the skull illustrates further the modern characteristics observed in the facial region of No. 792. The pituitary angle measured 121°

(fig. 2), so differing from the widely open angle in anthropoids, but the sphenomaxillary angle (90°) emphasises the alveolar prognathism, since this measurement is within the range of variation for the Australian aboriginal (Duckworth).

An examination of the sectional surface and interior of the cranium, reveals a number of features of interest. In the region of the bregma, the frontal bone attains a thickness of 12 mm. while both the parietal bone and the occipital in the region of the lambda are 11 mm. thick. In the vicinity of the inion, the bone is 18 mm. in thickness. These measurements are only slightly less than those of the Piltdown fossils. The texture of the diploe is, however, of a somewhat coarser nature in No. 792.

The endinion or mid-point of the cruciate eminence corresponds to a point on the planum nuchale which is 46 mm. from the opisthion. The inion is 66 mm. from the opisthion, a difference of 20 mm. (fig. 2). This low position of the posterior end of the transverse sinus closely approximates to the Neanderthal condition. Klaatsch found that the transverse sinus in the South Australian specimen (No. 1419, Stuttgart Museum) was 15 mm. below the superior curved line.

The inferior petrosal sinus on both sides forms a broad, deep channel roofed over by the petrous part of the temporal for 15 mm. on the right side and 12 mm. on the left side as it approaches the jugular foramen. The pituitary fossa is somewhat damaged, but is of normal proportions.

(*c*) *Palate and Mandible.* All the teeth have been lost post-mortem in No. 792. The remains of a well-marked processus molaris quarti are to be seen on each side. This process is exceeded in size by that in A. 11964 (Australian Museum), in which it is so large that it overlaps the palate bone posteriorly as a backwardly directed conical projection. The pyramidal process is comparatively well marked in our specimen, extending backwards 11 mm. from the level of the greater palatine foramen. There is a well-defined crest (torus palatinus medianus) in the mid-line of the posterior portion of the palate in several specimens, e.g., B. 10510 and A. 11964 both from the Australian Museum, Sydney, and in a young female from Queensland (*aet.* 24) (private collection). In No. 1308 (Medical School Museum) this torus expands anteriorly into a shield-like elevation of the maxilla which is limited laterally by a broad furrow, similar to the condition found in the Western Australian specimen (B. 10283) mentioned by Klaatsch, from the Australian Museum, Sydney (fig. 3 *a*). This torus maxillaris medianus may attain a width of 1 cm. after which it narrows towards the foramen incisivum. No. 1188, from the Medical School Museum, has a median furrow grooving the torus as in the South Australian described by Klaatsch. Extending transversely laterally from the torus maxillaris medianus at the boundary between the palatal and maxillary portions of the palate, there is in the last-named specimen a ridge (torus palatinus transversus) which reaches the medial boundary of the groove lodging the anterior palatine nerve and greater palatine artery. In No. 477,

also from the Medical School Museum, the torus transversus is continued laterally as a thin bar of bone which bridges over the groove (fig. 3*b*). From an examination of the Roth specimens, Klaatsch (12) is inclined to associate these spines and tubercles with the borders of the groove upon the palate. He states definitely that his experience failed to confirm Krause's statement that the occurrence of a trace of the torus palatinus transversus was frequent (p. 88). In the above-mentioned specimens examined by us, the transverse ridge is certainly independent of the palatine sulcus, though extending laterally to it, the site at which the junction occurs being marked by spinous processes at the borders of the groove. In Nos. 796 and 667 the arrangement of the tori of the palate is different from that above described. In these two specimens the median palatine torus, raised into a crest posteriorly, expands forwards into a V-shaped elevation, but instead of this elevation proceeding forwards as a median maxillary torus, the borders widen out at the boundary between

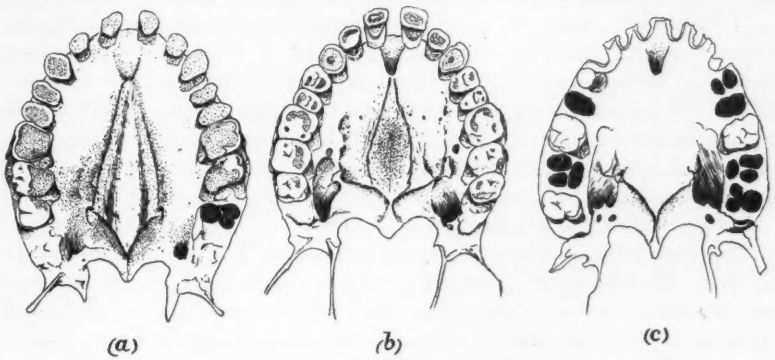

Fig. 3. Showing of arrangement of the tori palatini and maxillaris of the palate of Australian skulls. (*a*) No. 1308; (*b*) No. 477 (Medical School Museum); (*c*) No. 796.

the palatal and maxillary portions of the palate to become continuous with the transverse palatine torus. The maxillary torus is thus indistinguishable as a distinct elevation upon the palatal processes of the maxilla (fig. 3*c*). When well developed, these tori probably serve as additional supports for the force transmitted to the palate through the lingual roots of the molar teeth (fig. 9). In Nos. 620, 607 and 792 the tori are not well marked. There is a faint median crest representing the torus palatinus medianus posteriorly which diverges when traced forwards into a series of tubercles. These may be looked upon as constituting the torus palatinus transversus, which forms the posterior boundary of the flattened torus maxillaris medianus in the above-mentioned specimens. In No. 792 as in many Australian skulls a curved sharply defined crest for the tensor veli palatini (crista palatina transversa) is to be seen behind the transverse torus of the palate.

The shape of the palate indicates that this structure is of the modern type.

The palato-maxillary index of Flower is 120·6, so placing it in the brachyuranic group. The palatal width is 70 mm. and the palato-maxillary length is 58 mm.; these measurements are almost identical with those of the remarkable Mudgee skull described by Turner (71 and 58 mm. respectively) in which the index was as high as 122.

The mandible in No. 792 presents several features of interest in the region of the angle. The lower border curves gently backwards and inwards. The outer edge of this border is everted over an extent of 30 mm., the maximum projection being on the left side where it is 3 mm. (apophysis lemurica). On the inner surface of the angle there is a series of ridges (five on the right and eight on the left) here and there raised into as many spinous projections. These external and internal projections meet along the posterior border in a distinct tubercle. The same features are seen to an equal degree in No. 477; the apophysis lemurica is, however, developed to a much greater degree in the mandible belonging to No. 667 from the Hawkesbury District (N.S.W.).

Convex downwards the inferior border of the body continues backwards into the angle of the ramus which is gently rounded. A similar gentle curvature is present at the continuation of the alveolar margin into the anterior border of the ramus, but the general direction of the anterior border of the latter is approximately at right angles to the body. The medial aspect of the ramus shows anthropoid characteristics. An exceptionally well-marked ridge extends from below the tip of the coronoid process to the alveolar border. Behind this only the slightest indication of a fossa sub-coronoidea is present, but in front between this ridge and the anterior border of the ramus a deep groove is seen, the lower part of which groove is visible from the lateral aspect between the anterior border of the ramus and the socket for the third molar. This interval behind the 3rd molar (diastema molaris quarti) is 7 mm. as compared with 9 mm. in R. 2, the latter being one of Klaatsch's most marked cases. There is also a triangular backward extension of the alveolar margin (*circa* 6 mm.) claimed by Zuckerkandl (26) and Prof. J. T. Wilson (25) as indicating the previous existence of a fourth molar. Klaatsch regards the diastema as being a more important indication. It is to be noted that the two features are often present in the same skull (R. 2, R. 12, R. 57, R. 60 and the W.A. No. B. 10283, Sydney Museum). It is also to be noticed that the skulls with the most marked processus molaris quarti often have a correspondingly well-marked interval and triangular alveolar extension in the lower jaw (R. 2, R. 12, R. 44, R. 88 and No. 792).

R. 57 exemplifies the primitive parallel arrangement of the molar teeth on each side of the lower jaw, for as Klaatsch noted the distance between the first premolars was in this case 33 mm. and between the third molars was 40 mm. a difference of only 7 mm. In No. 792 the difference is 26 mm., the measurements being 24 mm. by 50 mm. respectively. These features and others, viz., the size of the ramus and the proportions of the coronoid and condyloid processus indicate that the mandible of No. 792 is distinctly modern.

The chin is moderately well marked (fig. 1) and the genioid spines present a considerable degree of prominence. The alveolar chin angle (Klaatsch) between the line of the alveolar border and the tangent from the mental protuberance to the anterior point between the incisors is 88°. This angle in our opinion does not give a conception of the degree of prognathism of the alveolar process of the mandible, for on inspection from behind, this process is seen to slope definitely forwards and upwards, corresponding with the alveolar prognathism of the maxilla already described. Except in a case such as No. 2165 (Medical School Museum) in which the chin is ill-defined and non-projecting, the development of the mental process obscures this forward slope when the mandible is viewed from the front and makes the alveolar chin angle approximate to 90°. We have therefore measured the angle included between the alveolar line and the line from the anterior point between the incisors to the lowest median point on the lower border of the body of the mandible in the mid-line (gnathion). The resulting angle in No. 792 is 76°, an angle which indicates more accurately than the "alveolar angle" the degree of alveolar prognathism.

In R. 2, in which the two lines used by Klaatsch are at right angles, we find the alveolo-symphysial angle to be 81°. This indicates the degree of forward slope of the alveolar process which is apparent on inspection. Examination of other Roth specimens confirmed this result. A consideration of the alveolo-symphysial angle together with the angle of alveolar prognathism of the maxilla, gives a true indication of the degree of "snoutiness" of the Australian aboriginal skull. It is specially worthy of note that the muzzle-like condition of the face may be present in an orthognathic skull such as No. 792 (cf. Topinard (19)).

II. The Cranial Skeleton

(*a*) *The Temporal and Sphenoidal Region.* The mastoid process is better developed in No. 792 than is usually the case in the aboriginal skull. The left process is somewhat more projecting but at a higher level than the right, the latter feature is part of a general asymmetry. The mastoid crest is continuous with the linea nuchae superior; though the latter is extremely well marked, the bridge uniting the mastoid process with it is not nearly so pronounced as in R. 60, especially referred to by Klaatsch. On this account the supra-mastoid crest is only moderately developed and an interval of 22 mm. separates it from the mastoid crest, again being unlike R. 60, in which the distance is only 10 mm.

In the region of the lambdoid suture is a rounded but well defined ridge, extending upwards and backwards for a distance of 21 mm. (fig. 6). Superiorly this ridge can clearly be traced into continuity with the superior temporal line, while inferiorly it blends with the crista mastoidea and passes towards the anterior border of the mastoid process. This then must be regarded as the actual termination of the superior temporal line in No. 792. Diverging from

this line in the region of the lambdoid suture as it is traced upwards, is a well-marked linea nuchae suprema. Thus the crista muscularis of the adult male gorilla is represented in No. 792 by four distinct lines—the temporal portion by the superior and inferior temporal lines and the occipital portion by the supreme and superior nuchal lines. The affinity with the anthropoid condition is shown by the close approximation of the posterior three lines for a distance of 50 mm. in the mastoid region (see fig. 7). Moreover in R. 60 and R. 24 there is a close approximation of the supra-mastoid crest to these three lines. In B. 3714 (Australian Museum), actual fusion of the four lines has occurred for a distance of 28 mm. producing a rough elevated area in the region of the asterion 14 mm. in width. This closely simulates the condition in the young anthropoid. Aboriginal specimens are thus met with in which the superior temporal line after continuing inferiorly, skirts the lambdoid suture in order to cut the parieto-mastoid suture about 10 mm. in front of the asterion. This may then become, as pointed out by Wilson (24), continuous with the mastoid crest (No. 792, No. 477, Medical School Museum; R. 2, R. 16, R. 24, R. 36, R. 60, No. 1245 and B. 3714, Australian Museum). In the majority of the above skulls including No. 792, the posterior inferior angle of the parietal bone is distinctly ridged by this continuation, recalling the considerable degree of prominence of the crista muscularis in the region of the asterion in anthropoids.

The parieto-sphenoid articulation is present and measures 5 mm. on the right side and 8 mm. on the left. The parieto-temporal suture has a more horizontal course than in the modern European, but the junction between the squamous and mastoid portions is clearly indicated (fig. 7). It is to be noted that the fronto-sphenoid articulation lies on a level with the zygomatico-frontal suture, i.e. at a somewhat lower level than is usually the case in modern skulls. The level of this suture is even still lower in the Anthropoids.

Klaatsch's method of measuring the post-orbital depression on the glabella-inion horizon was followed and the annexed table incorporates his figures for purposes of comparison:

	R. 24	No. 792	Pithecan-thropus	Spy I	Spy II
Post-orbital depression ...	90	91	87	104	103 mm.
Supra-orbital breadth ...	120	112	106	123	124 mm.
Index of the post-orbital depression $a \times 100/b$ ...	75	81·25	82·08	84·55	83·06
Distance of the post-orbital depression from the glabella	50	44	35	37	39 mm.

The above measurements illustrate the similarity of the Australian skull with the Spy, Neanderthal and Pithecanthropus specimens in the sphenoidal regions. None of the measurements, however, are outside the range of those found in the aboriginal skulls of the Roth collection. For instance, the distance of the post-orbital depression from the glabella, exceeds that found in the Spy specimens and also Pithecanthropus, all of which have a measurement

between 35 and 40 mm. Several skulls of the Roth collection were found by Klaatsch in which the distance was between 45 and 50 mm. (R. 24, R. 28, R. 57, R. 62). All these examples contrast with the European where the depression is usually placed closer to the glabella (Schwalbe, quoted by Klaatsch). Klaatsch measured the greatest supraorbital breadth, i.e., the distance between the ectorbital prominences which overhang the fronto-zygomatic suture. The degree of development of the external angular process is then given by comparing this measurement with the post-orbital diameter. The smaller the index the larger and more prominent is the external angular process and we may note that the index in No. 792 is slightly below that of Pithecanthropus and the Spy skulls.

(*b*) *The Cranial Vault.* In No. 792 the distance of the inferior temporal lines from the sagittal suture in a projection is 45 mm. in the frontal region (fig. 1); in the anterior parietal region it is approximately the same (45·5 mm.). The two temporal lines are separated from one another by a distance of 5 mm. even when only a short distance above the fronto-zygomatic suture. They diverge somewhat from one another and at the coronal suture are separated by an interval of 15 mm. On crossing this they both deviate upwards and skirt the upper margin of the parietal eminence.

The interval between the temporal lines is occupied by a well-marked bregmatic eminence forming a diamond-shaped area somewhat spread out both from side to side and from before backwards, approximating to the condition found in the W.A. B. 10283 (Australian Museum) skull. The anterior angle of this eminence which can be traced forwards to the supra-orbital depression forms a torus frontalis medianus.

Posteriorly the bregmatic eminence continues to the vertex (fig. 7); the highest point of the eminence is situated behind the bregma. The general form of the eminence in No. 792 is intermediate between the broad, flat elevation seen in the female Tasmanian in the Australian Museum and the more sharply defined eminence of Pithecanthropus. E. 11348 and S. 1158 (Australian Museum) have a similar eminence to No. 792, but it is separated posteriorly by a distinct depression from the vertex as in Pithecanthropus and R. 60. The receding forehead presents on either side of the torus frontalis medianus practically no signs of tubera frontalis.

In No. 792 the parietal eminences although present, are ill-developed, the interparietal diameter (117 mm.) being 15 mm. less than the greatest width (132 mm.) which coincides with the supramastoid breadth.

Turner (21), referring to the parietal bone in the Tasmanian aboriginal, states that "in the postero-parietal region a broad, shallow, median depressed area exists, bounded laterally by a low ridge on the parietal bone and along the middle of this depression the sagittal suture lies below the general plane of the vault." This condition is also to be observed in the skull of the Australian aboriginal, e.g., in No. 791, No. 618, R. 78, R. 45, R. 17, R. 14, R. 8 and R. 12, but is absent in No. 792.

The forward projection of the lateral part of the lambdoid suture found in the Neanderthal skull and some anthropoids, is remarkably well seen in No. 792 (fig. 8). This projection reaches to the same level as the lambda. In R. 7 and S. 1157 (Australian Museum) this projection is well shown on the right side while corresponding to it on the left side there is an intercalated bone. This association with intercalated bones is not uncommon as was pointed out by Klaatsch. There is a transverse occipital suture on both sides in No. 792 extending medially from the lambdoid suture for 15 mm.

An examination of the occipital region of No. 792 reveals a well-marked torus occipitalis transversus. Like several Roth specimens, e.g., (R. 60, R. 62, R. 80) the lower border of this torus in No. 792 is situated at a higher level than the sulcus transversus. The external occipital protuberance is not developed; the torus is continuous as an uniform elevation across the mid-line. In No. 477 (Medical School Museum) there is a torus of an even greater degree of development which presents two lateral tubercles. In the mid-line it also projects downwards into a V-shaped external occipital protuberance. The upper border of the torus in No. 792 representing the linea nuchae suprema is separated by a shallow groove from the remainder of the squama occipitalis. Two centimetres from the mid-line the torus presents on each side a prominent tubercle which is more projecting than the median portion of the torus. The internal aspect of the occipital at this point shows the impression of the occipital lobe of the brain, more marked on the left side, where the thickness of the bone is 10 mm.; this is to be compared with the maximum thickness in the mid-line which was found to be 18 mm. The lower border of the torus (linea nuchae superior) forms a thick rounded edge; a shallow groove separates it from the upper portion while it forms inferiorly a rolled projecting border, over which the planum nuchale passes into the squama occipitalis. The muscular impressions upon the planum nuchale reach only a moderate degree of development in this specimen.

The cubic capacity of No. 792 measured by chilled shot in the usual manner, was 1218 c.c. The water displacement of a cast made later after the skull had been sectioned was 1211 c.c. Turner (20) found that the mean cubic capacity of 34 adult crania in his series was 1230 c.c. Duckworth determined the average cranial capacity of the adult Australian aboriginal to be 1246·5 c.c. from measurements on 150 skulls.

The skull is markedly dolicho-cephalic, the cephalic index being 65·02. It is also markedly phenozygous as already indicated (fig. 9).

The General Relative Proportions of the Cranium

Horizontal curves on the glabella-inion plane, on a plane 20 mm. above this and at the point of deepest depression of the nose, were made with the aid of Lissauer's diagraph, the maximum projection of the superciliary ridges being also shown (fig. 2).

The usual flattening of the temporal and sphenoidal regions found in

Australian aboriginals is not so marked in No. 792, which approaches the condition met with in the exceptions in the Roth collection mentioned by Klaatsch (R. 2, R. 16 and W.A. B. 10283) which he points out is a permanent feature. It is to be noted that the asterionic diameter exceeds the stephanic by 11 mm. Transverse curves were drawn in a like fashion through the bregma and the vertex with the skull oriented in the glabella-inion plane (fig. 5). Both the height of the bregma (91 mm.) and the vertex (98 mm.) are well within the range found in Australian aboriginals.

The maximum occipital point coincides with the inion. A massive torus combined with an elevation of the inion gives a pithecoid appearance to the occipital region. Coincidence of the inion and maximum occipital point which

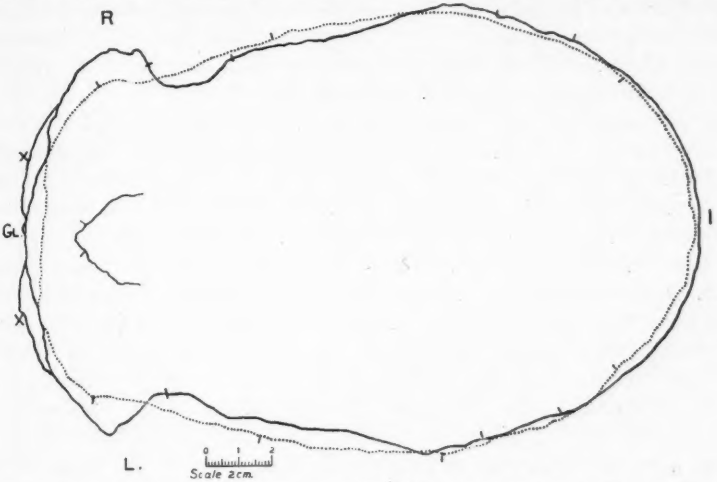

Fig. 4. Horizontal sections of Australian skull (No. 792). (*a*) At the level of the glabella-inion plane (interrupted line). (*b*) On a plane 20 mm. above the glabella-inion plane (dotted line). The greatest forward projection of the superciliary ridges is also indicated and the most depressed point of the nasal region. Also the position of the various sutures as they occurred.

is seen in Pithecanthropus and the Neanderthal is also exhibited in R. 2 and R. 60 (Klaatsch), R. 9, S. 1158, E. 11348, No. 791, No. 796 and a Tasmanian calvarium, No. 1254 (Australian Museum). In consequence of this, the maximum cranial length in these skulls is identical with the glabella-iniac length. In the specimens mentioned this length ranges between 182 mm. (R. 2) and 192 mm. (F. 11348), the Tasmanian specimen measuring 184 mm. and Pithecanthropus 181 mm. No. 792 on the other hand has a length of 203 mm. The longest Australian male cranium described by Turner measured 200 mm. (Challenger series 20). This length was considered by Turner to be remarkable. He quotes, however, cases which had an even greater length, e.g., Miklucho-Maclay's specimen which measured 204 mm. in length and that of Davis 210 mm. The sutures in skull No. 792 though simple, are normally developed.

There is no sign of closure of the sagittal suture as in Miklucho-Maclay's specimen. The maximum occipital length in No. 792 exceeds in length the Neanderthal (200 mm.), Spy I (200 mm.), and Spy II (198 mm.). It will, therefore, be seen that the calvarium of No. 792 resembles the Neanderthal fragment, both in its absolute length and in the fact that the maximum occipital point coincides with the inion. The general appearance of the cranium, however, differs from the Neanderthal fragment, in that platycephaly is apparently not a marked feature in No. 792 and the marked lateral bulging posteriorly is not reproduced. On measurement, the cephalic and vertical indices are found to be approximately equal, 65·02 and 65·07 respectively.

It is interesting to note that there is combined with this dolicho-platycephaly, marked projection of the superciliary ridges and glabella. In regard to this Turner (19, p. 49) says, "the strongly projecting supraciliary ridges and glabella which have been described as characteristic features in the dolicho-platycephalic crania, are by no means confined to them."

It may be noted that Huxley's Western Port skull also had a cephalic index of 73 and a vertical index of 73·6 (8, 9). Quatrefages and Hamy (15) classify the skull presented by M. Erklund to the Museum Retzius as dolicho-platycephalic. The cephalic and vertical indices are 64·6 and 64·1 respectively. He contrasts these measurements with those of a skull of the ordinary Australian type, in which the length-breadth index is 67·0 and the vertical index 73·19. In this connection a *resumé* may be given of the characteristics of a skull from Port Fairy, Victoria, in the Australian Museum (No. 1245) and described by Quatrefages and Hamy. The glabello-iniac length is 194 mm. while the maximum length is 206 mm. due to a backward bulging of the squama occipitalis. The maximum breadth, which is the supra-mastoid diameter, is 142 mm. compared with a basi-bregmatic height of 131 mm., giving a cephalic index of 68·44 and a vertical index of 63. These indices indicate a condition of marked dolicho-platycephaly. A fossa pre-lambdoidea is present in the Port Fairy skull as would be expected on account of the marked backward bulging of the squama occipitalis, the glabella-lambda length (200 mm.) being greater than the glabella-inion length (194 mm.). This fossa is also well represented, however, in No. 792, although the squama is directed not backwards but slightly forwards, the glabella-lambda length (194 mm.) being less than the glabella-inion length (203 mm.).

An idea of the direction of the squama is obtained by measuring the angle between the glabella-inion and inion-lambda, which is 72° compared with 67° in the Neanderthal and Spy I skulls, 70° in Spy II and 71° in R. 2, the lowest of the Roth series. The smallness of this angle is another indication of the primitive formation in the occipital region. The opisthionic angle is 33°. The planum nuchale slopes upwards and backwards to the inion (in the median plane). It has an absolute length greater than that of the squama occipitalis, the measurements being respectively 66 mm. and 56 mm. These two features further emphasise the pithecoid appearance.

The curvature of the occipital measured by the distance of the lambda-inion line from the most prominent point of the curvature of the planum occipitale is shown in No. 792 to be intermediate between Pithecanthropus and the Neanderthal specimen (Table VII). The preservation of this small degree of curvature is not uncommon in aboriginal skulls as shown by the Roth collection.

The angle between the glabella-inion and the glabella-lambda lines is below the range for the Australian and other races (17°–22°; Klaatsch). It is the same as that of the Neanderthal fragment, viz. 15°. This angle points to the comparative shortness of the planum occipitale which subtends this angle.

In addition to the primitive formation in the occipital region, there is, as has already been pointed out, a remarkable recession of the forehead. The following measurements of the bregma-glabella-inion angle (Schwalbe) are significant: No. 792, 50°; R. 2, 56°; South Australian, 51°; West Australian, 56°; Pithecanthropus, 41°; Neanderthal, 45°; Spy I, 46°; Spy II, 47°; Klaatsch stated that the range for Australian aboriginals was 51° to 62°. However, fig. 8 *a* of Berry and Robertson's tracings of Australian crania(3) exhibits an angle of 49°. From the above figures it will be seen at once that the forehead region in No. 792 approaches more closely to that found in the Neanderthal race than in R. 2, the S.A. (Stuttgart) and the West Australian (the lowest recorded by Klaatsch). In order to indicate more fully the slope of the forehead, the index of curvature of the frontal is recorded in these cases, i.e., the comparison between the glabella-bregma length and the distance of this line from the most prominent point of the frontal. Like R. 2 and the W.A. No. 792 falls within the range of variation of the Neanderthal specimens. On the other hand the South Australian specimen has a considerable degree of curvature of the frontal despite its low bregma-glabella-inion angle, a fact which illustrates the necessity of measuring the index of curvature of the frontal. The degree of frontal slope may be measured also by estimating Schwalbe's forehead angle, which is included between the glabella-inion line and the tangent from the glabella to the most prominent part of the surface outline of the frontal. This angle is 98° in the S.A., as compared with 67° in Spy II. In No. 792 it is only 70°, which indicates a stage of forehead slope between the lower limit for modern races and the Neanderthal race. The W.A. skull has the lowest measurement of any Australian skull of the Australian Museum series, viz., 74°. The very low angle in No. 792 is due to the fact that the point of maximum curvature of the frontal is situated more posteriorly than in some specimens which have a lower index of curvature.

In R. 2 the degree of frontal curvature is less than in No. 792, for the maximum elevation of the frontal above the glabella-bregma chord is only 13 mm. in the former compared with 15 mm. in the latter; the index obtained by comparing this with the length of the chord being 12·5 and 13·04 respectively. The forehead angle in R. 2 is, however, 79°, due to the fact that the

maximum point of curvature is situated more anteriorly than in No. 792. The more posteriorly this point is placed, the more primitive is the appearance of the sloping forehead. Comparable to No. 792 in this respect is the West Australian skull, which has been seen to have a forehead angle of 74°, the index being 13·2.

The bregma-nasion-inion angle was measured in No. 792 to compare the degree of slope of the forehead with that of the New South Wales specimen (XXIX. B. 12, Turner series) described by Cunningham (5). It was found to be 54°, as compared with 53° in the New South Wales specimen. Applying the method used by Cunningham for obtaining the frontal index of curvature, viz., comparison of maximum height of the frontal above the line joining the nasion and bregma, with the distance between these two points, we found that this index in No. 792 was 20. In the New South Wales specimen this index is 15. These two measurements indicate a more receding forehead in the skull described by Cunningham than in No. 792.

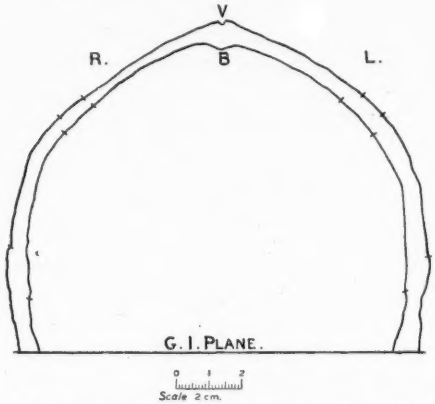

Fig. 5. Vertical sections of Australian skull (No. 792) from the glabella-inion plane to the bregma (*B*) and the vertex (*V*). The temporal lines and squamosal suture are indicated.

In No. 792 the height of the bregma above the glabella-inion line is 90 mm. giving an index when compared with the glabella-inion length of 44·23. The lowest index in the Roth series was 47·25 (R. 2). Klaatsch (12, p. 139), however, found that the South Australian specimen had an index of 44·79. This latter skull and also one from North Queensland, he found "nearest to the type of fossil European man" of the skulls he examined.

The height of the vertex of No. 792 is 98 mm. giving an index when compared with the glabella-inion length of 48·27, which is less than that of the South Australian skull. It is to be noted that both the index of the height of the bregma and of the vertex of No. 792 reach their low limit on account of the great glabella-inion length.

Summary and Conclusions

The outstanding features of the skull No. 792 are:

(i) The general massiveness of the skull including the great thickness of the cranial vault.

(ii) The receding forehead.

(iii) The great absolute length of the cranium.

(iv) The massive undivided tori supraorbitales, and the marked projection of the glabella in the region of which unusually large frontal air-sinuses separate the two tables of bone.

(v) The pithecoid conformation of the occipital region and the presence of a well-defined torus occipitalis.

The face is less primitive than the cranial vault exhibiting orthognathism and a leptorrhine nasal region.

Special reference has been made to the Neanderthaloid features of the specimen. The resemblances of the cranium to the Neanderthal specimen is remarkable when the marked contrast of the general skeleton of the two types is kept in mind. We must regard the cranial resemblances as an expression of the principle that descendants of a common ancestor show a tendency to develop independently similar features.

The Neanderthaloid features of No. 792 are as follows:

(1) The degree and projection of the glabella and tori supraorbitales, the latter being undivided (Type III, Cunningham).

The index of post-orbital depression is 81·25 (Pithecanthropus, 82·08; Spy II, 83·06) and the distance of the post-orbital depression from the glabella is 44 mm. (Pithecanthropus, 35; Spy II, 39).

(2) The presence of the fossa supraglabellaris and sulci supraorbitales.

(3) The degree of forehead slope. (Bregma-glabella-inion angle 50° (Spy II, 47°); Schwalbe forehead angle 70° (Spy II, 67°). Index of curve of frontal 13·04 (Neanderthal, 13·39; Spy I, 10·10; Spy II, 15·92).)

(4) The great length of the precerebral part of the roof of the orbit. (No. 792, 25 mm.; Neanderthal, 20 mm.)

(5) The presence of a bregmatic eminence.

(6) The presence of the torus occipitalis transversus with tubercles situated laterally.

(7) The low position of the endinion (20 mm. below inion).

(8) The contour of the lambdoid and temporal sutures.

(9) The rounded outline of the temporal and sphenoidal regions, as depicted in horizontal and vertical sections.

(10) The coincidence of the inion and maximum occipital point, combined with the great absolute length of the glabella-inion line (203 mm.).

(11) The fact that the skull is dolicho-platycephalic as shown by the low cephalic index (65·02) and the equality of the cephalic and vertical

indices, although the flattened appearance of the Neanderthal is absent.

(12) The forward slope of the planum occipitale as measured by the glabella-inion-lambda angle, viz. No. 792, 72°; Spy II, 70°; Neanderthal and Spy I, 67°.

(13) The low indices both of the height of the bregma (44·23) and of the vertex (48·27).

(14) The angle between the glabella-inion and the glabella-lambdaines (15°) is the same as in the Neanderthal.

Of the above features, the development of the tori supraorbitales and glabella, the fossa supraglabellaris and sulci supraorbitales, and the well-defined diamond-shaped bregmatic eminence, show a resemblance to Pithecanthropus.

It is thus seen that it is the calvarium of No. 792 which retains primitive features. The facial skeleton presents paradoxically modern features. Therefore this specimen illustrates, as Turner (20, p. 49) indicated, that specialisation in some directions may be accompanied by a marked lack of specialisation in other respects in one and the same skull.

The general survey of Australian skulls, undertaken for purposes of comparison with No. 792, led to conclusions which may be summarised as follows. The diamond-shaped appearance of the face, commonly found in the Australian, owing to the prominence of the zygomatic bones and curvature of the zygomatic arch, is developed as a result of the increase in these bones to provide a base of resistance during mastication, and to support the masticatory muscles. Further the explanation of the rolled character of the inferolateral margin of the orbit was attempted by correlating this condition with the size and degree of wearing of the teeth. Finally the considerable variability in the degree of development of the infraorbital fossa is found to be due to the varying conditions connected with the direction of the masticatory thrust from the different groups of teeth.

The principal measurements of No. 792 are:

Cubic capacity, 1211 c.c.; maximum length (glabella-inion), 203 mm.; maximum breadth, 132 mm.; cephalic index, 65·02; basi-bregmatic height, 133 mm.; vertical index, 65·07; auriculo-bregmatic height, 111 mm.; glabella-lambda line, 194 mm.; nasion-inion line, 195 mm.; basion-nasion line, 107 mm.; prosthion-basion line, 99 mm.; minimum frontal breadth, 90 mm.; maximum frontal breadth, 103 mm.; asterionic diameter, 111 mm.; interparietal diameter, 117 mm.; stephanic diameter, 100 mm.; supramastoid breadth, 132 mm.; nasal height, 55 mm.; nasal width, 26 mm.; nasal index, 47·2; height of apertura piriformis, 35 mm.; index of apertura piriformis, 74·3; height of choanae, 39 mm.; width of choana, 19·5 mm.; orbital height, 35 mm.; orbital width, 39 mm.; orbital index, 89·75; minimum interorbital distance, 18 mm.; inter-zygomatic breadth, 139 mm.; palatal length, 52 mm.; maxillary breadth, 94 mm.; length of os palatinum, 17 mm.; depth of palate at M. 1,

13 mm.; basi-alveolar length, 100 mm.; basi-nasal length, 105 mm.; gnathic index, 95·23; symphyseal height, 27 mm.; angle of the ascending ramus, 113°; coronoid height, 73·5 mm.; minimum breadth of the ramus, 32 mm.; bigonial width, 104 mm.; inter-coronoid width, 104 mm.; inter-condyloid width, 119 mm.

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EXPLANATION OF FIGURES

As. Asterion; *B.* Basion; *Br.* Bregma; *End.* Endinion; *Gn.* Gnathion (Wilder); *Gl.* Glabella; *I.* Inion; *L.* Lambda; *M.F.* Mental Foramen; *N.* Nasion; *Ns.* Nasospinale; *O.* Opisthion; *Po.* Porion; *Pr.* Prosthion; *Ps.* Prosphenion; *Sph.* Sphenoidale; *V.* Vertex.

Figs. 6–9. Various normae of Australian skull (No. 792).

SKULLS REFERRED TO IN THE TEXT

I. *Anatomy Department Collection*

No. 792. Tamworth, N.S.W. No. 607. Little Manby, Sydney, N.S.W. No. 618. Little Manby, Sydney, N.S.W. No. 620. Botany, Sydney, N.S.W. No. 667 (Hawkesbury District, N.S.W.). No. 791 (Dashino Downs) Queensland. No. 793. Central Australia (?). No. 795. N.S.W. No. 796. N.S.W. (?).

II *Medical School Museum*

No. 477. Kyogle, N.S.W. No. 1188. Northern Australia. No. 1308. Port Jackson, Sydney, N.S.W. No. 2165. No data. No. 2355. Port Hacking, N.S.W. No. 2356. Port Hacking, N.S.W.

III. *Australian Museum, Sydney*

B. 10283. ♂, Western Australia with fourth molars in upper jaw. No. 1245. Port Fairy, Victoria. E. 11348. Lake Victor, N.S.W. S. 1157. Jervis Bay, N.S.W. S. 1158. Gurdogai, N.S.W. B. 3714. No data. S. 404. Tasmanian No. 1254. Tasmanian B. 10510. Cairns, Queensland. A. 11964. Queensland.

A. 11964; R. 2, ♂; R. 5, ♂, R. 7, ♂; R. 8, ♀; R. 9, ♂; R. 10, ♂; R. 12, ♀; R. 14, ♂; R. 15, ♂; R. 16, ♂; R. 17, ♂; R. 24, ♂; R. 25, ♂; R. 28, ♂; R. 35, ♂; R. 36, ♂; R. 38, ♂; R. 39, ♂; R. 44, ♀; R. 45, ♂; R. 49, ♀; R. 57, ♂; R. 58, ♂; R. 60, ♂; R. 62, ♂; R. 69, ♂; R. 78, ♂; R. 80, ♂; R. 82, ♀; R. 87 (child); R. 88, ♂, Queensland.

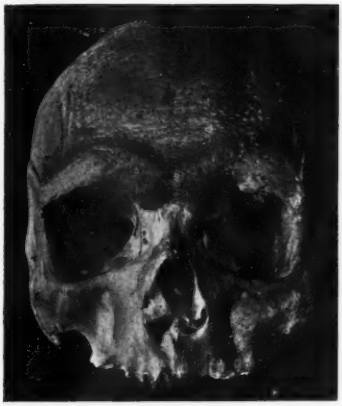

Fig. 6

Fig. 7

Fig. 8

Fig. 9

ODONTOLOGICAL ESSAYS

By L. BOLK, M.D.

Director of the Anatomical Institute of the University of Amsterdam

FIFTH ESSAY

ON THE RELATION BETWEEN REPTILIAN AND MAMMALIAN DENTITION

In the previous essay I expressed my views upon the relationship between the simple teeth of Reptiles and the composite teeth of Mammals, and the manner in which the latter were evolved from the former. Although I made some allusion to the relationship between reptilian and mammalian dentitions as a whole yet I pleaded that criticism of the views expressed in that essay be suspended until my more complete considerations on the dentitions of the two groups were published.

In the present essay I will endeavour to make good the contention that tooth-succession in the mammal is a phenomenon entirely different from that occurring in the reptile. The contention is based upon certain hitherto undiscovered facts, ascertained as a result of an exhaustive investigation on tooth development in reptiles.

In comparing reptiles and mammals the Marsupials will not be taken into account. As is well known the marsupial dentition is entirely different from that of mammals and any attempt to homologise the functional dentitions of these animals is a task of considerable difficulty. The reason for such difficulty will become apparent later, but I may be justified in eliminating its present consideration on the following grounds. An investigation on the development of the teeth in marsupials has convinced me that these more primitive mammals occupy, as regards their dentition, a position intermediate between the Reptilia and the Eutheria; in other words the Metatheria resemble the reptiles in some respects and the Eutheria in others. This fact appeared to me of such importance as to require a special essay upon tooth-development and tooth-succession in marsupials. This essay will be published in due course.

A short summary of current opinion concerning the relationship between tooth-succession as it occurs in reptiles and placental mammals respectively may precede the exposition of my own views.

The fundamental difference between the dentitions of the two groups is shown by the fact that in reptiles tooth-succession is unlimited, whilst in most Placentalia one succession of teeth alone eventuates and in some of them no succession occurs at all. These differences are expressed by the terms: polyphyodont, diphyodont and monophyodont. The two dentitions of diphyo-

dont mammals are distinguished as the milk dentition and the permanent dentition respectively.

In the case of monophyodontism it is not always certain to which of the two the functional dentition belongs. For instance Kükenthal considers the functional teeth of Cetaceae to be a milk dentition. In other cases, as in Talpa, tooth-succession occurs before birth, and the functional teeth belong to a second or permanent series. The investigations of Leche show that the functional dentition of Erinaceus is mixed, containing elements of both dentitions. Such cases, however, may be regarded as exceptional, as two dentitions, a milk and a permanent, occur normally in mammals. It is commonly held that the two dentitions of mammals are homologous with two tooth-generations of reptiles, that the diphyodontism of mammals proceeded from the polyphyodontism of reptiles by a diminution of the unlimited succession of teeth peculiar to these vertebrates; and that the difference between the two groups of vertebrates is of a purely quantitative nature, monophyodontism being considered as a further stage in the process of diminution. This view is supported by Marett Tims, who summarises current opinion by presenting in Tomes' *Manual*, 7th edition, p. 362, a very suggestive diagram of the interpretation of mammalian dentition.

In a recent communication Broom[1] lays stress upon a fact which apparently establishes the correctness of the above mentioned relationship between mammalian diphyodontism and reptilian polyphyodontism. Of all reptiles the extinct group of Cynodontia are recognised as exhibiting the nearest relationship to mammals. Broom, describing tooth-succession in a nearly adult specimen of *Diademodon platyrhinus*, demonstrates that there is close agreement between it and the normal appearances in mammals. However, I am of the opinion that this agreement is insufficient to prove the identity of the process of tooth-succession in mammals and reptiles. Broom's observations prove that in Cynodontia a succession of teeth occurs but once only. Such a phenomenon is by no means remarkable as in certain recent reptiles, Calotes may be cited as an example, tooth-succession occurs very slowly indeed. That some reptile or other exhibits but one single tooth change is not conclusive evidence that the character of this process in reptiles and mammals is identical. Nevertheless, the succession of teeth in Cynodontia seems to me a phenomenon worthy of careful consideration, since the possibility of the process of tooth chance in this group of reptiles harmonising in some respects with that in marsupials must be taken into account, as the marsupials occupy a position intermediate between the Placentalia and the Reptilia.

The hypothesis of a direct relationship between reptilian and mammalian tooth-succession has already been accepted as a dogma and its truth has never been questioned. Labouring under the thraldom of this conviction many investigators have studied tooth-development in mammals with the avowed

[1] "On Evidence of a mammal-like dental succession in the Cynodont Reptiles." *Bull. Am. Mus. Nat. Hist.* vol. XXXII. 1913.

object of discovering vestiges of additional dentitions. A considerable literature exists in which the germs of hypothetical premilk or post-permanent dentitions are described. While agreeing with those authorities who throw doubt upon the validity of the appearances described as proving such additional dentitions, I further deny their possibility on fundamental grounds. My opinion as to the significance of epithelial excrescences and protuberances differs entirely from that of other investigators who interpret them as vestigial germs of an abortive dentition. I have already demonstrated that the epithelial formations regarded as evidence of a premilk dentition are in reality partly rudiments of the teeth glands in reptiles (*vide* Essay III) and partly fragments of the external enamel strand (*vide* Essay II). My views concerning the germs which are presumed to indicate a potential post-permanent dentition, will appear in a subsequent essay.

With this introduction the discussion of the subject matter of the present essay can now be approached.

If the first toothgerms appearing upon the dental lamina of a reptilian embryo be carefully studied one is struck by the fact that these germs do not all behave in the same manner. In order to prove this I will describe the peculiarities of the first teeth in the upper jaw of a *Crocodilus porosus*. In fig. 108, eight sections through the germ of such a tooth are represented. In

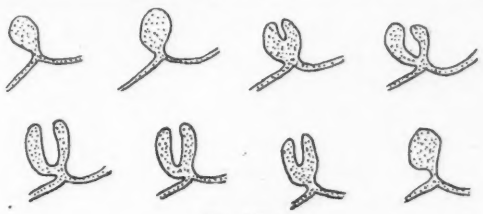

Fig. 108.

the first section the toothband, still rather short in this stage, is, as a whole, swollen and its thickening is apparently symmetrical. The dentine-papilla, seen in the further sections, also seems to be symmetrically disposed, and has apparently pushed its way in at the distal end of the thickening, the enamel-organ having assumed the well known form of a bell.

The toothgerm next in order, of which eight sections are also represented (fig. 109), shows, however, a somewhat different relationship between the dentine-papilla and the enamel-organ. The tooth-band is swollen up, as in the first germ, but in this case the thickening is evidently asymmetrical. Further it must be particularly noticed that the dentine-papilla has pushed its way into the lateral or buccal side of the enamel-organ and not at its distal end.

The different behaviour of the dentine-papilla in the two toothgerms gives one the impression that one of the toothgerms is formed from the border of the dental lamina, the other from its buccal side. As far as the latter is

concerned this is really the case, the toothgerm represented in fig. 109 being without any doubt a formation on the lateral side of the toothband.

I will postpone for the time being the consideration of the real topography of the toothgerm represented in fig. 108.

I have observed this different behaviour of the toothgerms and their relationship to the toothband, not only in Crocodilia, but also in a number of other

Fig. 109.

Reptilia, in which I have had the opportunity of examining the earliest stages of development. It is most noteworthy that in all the cases I have studied the two types of toothgerm, which may be distinguished as "terminal" and "parietal" respectively, show a regular alternation. A terminal toothgerm is always followed by a parietal, the next in order is a terminal and so on. The following may be taken as examples of this phenomenon.

Fig. 110 represents sections through four consecutive toothgerms in the lower jaw of a young *Gecko verticillatus*. The first represents a "terminal" germ with the dentine-papilla pushed into it. Between this germ and the next a section of an interspace is shown (110 *b*). Fig. 110 *c* illustrates a section of the next germ. By comparing 110 *c* with 110 *a* two facts can be readily appreciated. In the first place, the germ of 110 *c* is developed from the buccal side of the dental lamina which ends with a so-called free border which appears as an outgrowth on the lingual side of the toothgerm. That such a free border is formed, is easily demonstrable in fig. 109. The toothgerm in 110 *c* represents a somewhat later stage of development than that of the germ in fig. 109, but in both the dentine-papilla may be seen projecting into the buccal side of the toothband. From its earliest beginnings the lingual wall of this toothgerm is obviously thicker than its buccal. Near to the free edge of this thickened wall there appears a furrow by means of which the enamel germ becomes more completely separated from the dental lamina. The cell-mass disposed to the lingual side of this furrow, is the so-called free border of this lamina. The typographical relationship of the toothgerm to the dental lamina is obviously different in 110 *a* to that in 110 *c*. A second point worth noting is that the

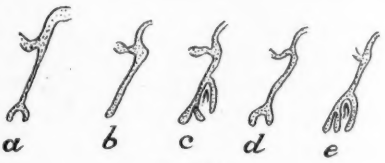

Fig. 110.

parietal toothgerm of 110 *c* has attained a more advanced stage of development than that in 110 *a*, since in the former the summit of the dentine-papilla is already covered by a thin layer of hard tissue which is lacking in the latter.

An interspace intervenes between the toothgerm in 110 *c* and the next tooth 110 *d*, which is a terminal one and resembles that of 110 *a* in all respects. A third interspace follows and separates it from another parietal toothgerm 110 *e* in which the formation of dentine has commenced as in 110 *c*.

The sections shown in fig. 110 confirm the fact that in its earliest stage of development the dental lamina produces two types of enamel-organ, a terminal and a parietal, and the two types exhibit a regular alternation. The parietal germs are somewhat older than the terminal and from this it may be concluded that the formation of the former begins before that of the latter. This conclusion is strengthened by the following observations. During development the dental lamina lengthens in a backward direction, its posterior part being younger than its anterior. If the hindmost part of the toothband in a young reptilian embryo be examined the parietal germs will be found to exhibit earlier stages of development, while the terminal germs have not yet appeared.

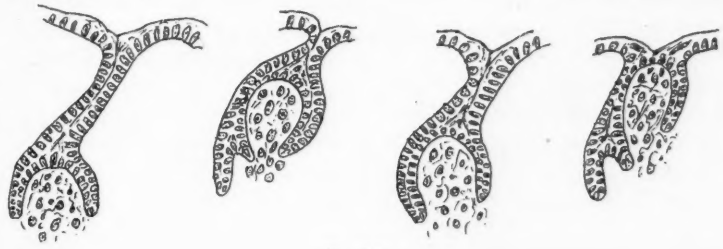

Fig. 111.

There are other features of the posterior part of the toothband indicating that it is younger than the anterior part.

Fig. 111 illustrates another example demonstrating the two types of dental germs. In this figure sections through four consecutive germs of a young embryo of *Gongylus ocellatus* are represented. These figures are intentionally drawn on a large scale as they will be utilised for the study of the structure of the dental lamina.

These sections again supply evidence of the existence of the two types of the earliest germs produced by the toothband. It may be specially noted that the so-called free margin, in association with the parietal germ which is situated very definitely upon the buccal side of the toothband, is differentiated very early. Further the alternation of the two types is manifest.

The structure of the dental lamina will be discussed in detail later, but certain remarks concerning it may be interpolated here. A striking feature of the toothband observable in all reptilian embryos and sometimes even in very young mammalian embryos is, that it is an actual folding of the superficial

epithelium sinking into the subjacent mesenchyme. This organ consists therefore of a double lamina and is composed of an outer or buccal plate and an inner or lingual plate.

I am influenced by two reasons for laying stress upon this fact. In the first place it teaches us the real nature of the toothband and the relationships of the toothgerms. As fig. 111 clearly shows the buccal plate of the toothband alone possesses a formative function, the enamel-organs being exclusively derived from it. This is incontrovertibly the case as far as the parietal germs are concerned and is also true as regards the terminal germs. The small club-shaped thickenings, representing the earliest stages of development of these germs, appear near to, but not quite at the border of the fold. Further the dentine-papillae grow into the buccal aspect of these germs. The tooth lamina is more rightly called the toothfold, a term used by the earlier morphologists. The expression "toothband" fails to convey its true character and the German term "Ersatzleiste" is, as will be shown later, absolutely misleading.

The two epithelial layers contributing to the dental lamina are not equivalent; the lingual layer is passive and takes no part in the formation of the enamel-organs.

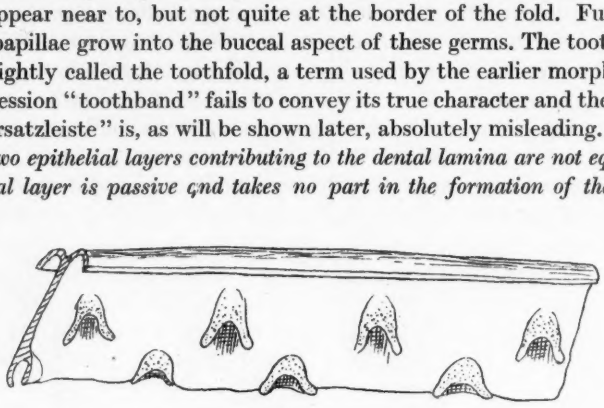

Fig. 112.

In reptiles the enamel-organ is produced by the buccal layer exclusively. This fact is of the greatest interest, since it implies a complete harmony between the dentition of the reptiles and that of the lower vertebrates, more especially of the Selachii. To this point I will revert later. I could add many more examples illustrating the same points as those given in figs. 108 to 111, but it would be superfluous to do so. The structure of the toothband in reptiles and the relationship of the toothgerm to it, as I have formulated them, are not exceptional but are the rule as may be easily verified by anyone possessing suitable material for examination.

That the toothgerms which I have termed "terminal" may be the succeeding teeth of the parietals is a question which may naturally present itself to my readers. Having made this possibility a matter of special investigation I can state definitely that, as regards tooth replacement, there is no relationship whatever between the parietal and terminal teeth.

The first fundamental fact elucidated by my researches is that in reptiles not only are there two types of toothgerm but each type is disposed in a different manner on the toothband. Fig. 112 is an attempt to represent diagrammatically a portion of the toothband of a young reptilian embryo viewed

from the buccal side and showing the arrangement of the toothgerms. This figure demonstrates that, in its earliest stage of development, the dentition of reptiles consists of two rows, the components of which alternate regularly. These rows I shall distinguish as "Odontostichi," and term the dentition as a whole "distichical." Of the two rows I name the one consisting of the parietal germs "Exostichos" as it is disposed nearer to the surface, the other consisting of the terminal germs "Endostichos." The teeth of the exostichos appear earlier than those of the endostichos, the development of the latter, as compared with the former, being always somewhat behindhand.

We must now consider how the two types of toothgerms participate in the building of the functional dentition. As far as the arrangement of the teeth upon the jaws is concerned there is no indication of the distichical character of the dentition, since the teeth are placed in a single series. When, however, the method of tooth change is closely examined the distichical character becomes apparent in a somewhat unexpected manner. Stress has already been laid upon the fact that in reptiles the endostichical teeth are not the successional teeth of the components of the exostichos. The latter are older than those of the endostichos and are situated nearer to the border of the jaw. As they move towards the surface they reach this border and attach themselves to it before the elements of the endostichos. In the meantime, as a result of the elongation of the jaw, the dental interspaces widen. Later the teeth of the endostichos fill up these interspaces, an endostichical tooth pushing itself in between two exostichical teeth at regular intervals. As a final result the functional dentition consists of a single row. This eventual monostichical arrangement is apparent only, the primitive distichy having become obscured. The exostichical and endostichical teeth alternate regularly and function simultaneously. This condition constitutes the fundamental difference between the dentitions of reptiles and of mammals respectively. As two rows of teeth both take part in its construction the dentition of the reptile may be termed "hamastichical."

I shall endeavour to prove in a subsequent essay that the marsupial dentition is also built up of two rows, but the process is incomplete and the mixing of the elements of the two rows is irregular. In order to distinguish the regular arrangement found in the reptile where a tooth of the endostichos regularly intrudes into an interspace of the exostichos the dentition of the reptile may be further defined as "isocrasic hamastichical."

To render the exposition of the developmental history of the reptilian dentition as simple as possible I have omitted one phenomenon observable in nearly all reptiles. The first teeth appearing in the embryo do not as a rule attain maturity, but calcify prematurely, lose their connection with the dental lamina, are surrounded by mesenchyme, and finally atrophy completely. This fact is only mentioned here incidentally and does not modify in the least my line of argument concerning the relationships between reptilian and mammalian dentitions. For a more complete story of the development

of reptilian dentitions I would refer the reader to a paper of one by my pupils[1].

The manner in which tooth replacement occurs in reptiles may now be discussed.

In my fourth essay (*q.v.*) I showed that the teeth are produced from a matrix in a manner comparable to the development of hairs and scales, ectodermal organs which also exist temporarily and are cast off periodically. A succeeding hair or scale arises upon the same papilla as its predecessor, and is formed from the same epithelial matrix.

The succession of teeth in reptiles occurs in a similar manner. The potentiality of producing teeth is concentrated in a number of well limited areas of the toothband. Such an area I will call a tooth matrix. These matrices are anatomically indistinguishable and they consist of the same epithelial elements as those of which the whole lamina is composed. The conclusion, that such tooth matrices exist, is drawn from the fact that on the same spot on the dental lamina, where a tooth is formed a succeeding tooth appears after a longer or shorter period. Further, in some few cases the dentine-papilla of a very young tooth and that of its predecessor are not sharply separated from one another, but a slight connection exists between them. I will allow that the idea of tooth matrices is hypothetical, but in the course of this essay I hope to establish certain facts which render their existence unquestionable.

If it be admitted that the toothband is the bearer of the tooth matrices the functional significance of this band appears to be somewhat different from that generally ascribed to it. Its function is obviously to carry the tooth matrices from the surface into a deeper and more protected situation.

I have shown that the first teeth produced by the dental lamina are arranged into two rows, an exostichical and an endostichical. Combining this fact with the doctrine of tooth matrices I arrive at the following conception. In the dental lamina of the reptiles there are two rows of matrices, an exostichical and an endostichical and the components of the two rows exhibit a regular alternation.

Tooth change takes place in reptiles in the following manner. After a matrix has produced a tooth, it enters into a state of inactivity during which the tooth produced moves towards the surface and becomes attached to the jaw. This state of inactivity lasts for a longer or shorter period, but in due time the matrix again becomes active and produces another tooth. The second tooth in its turn moves towards the surface, approaches the border of the jaw and pushes out its predecessor. By a repetition of this process a tooth matrix is continually producing new teeth during the existence of the animal in precisely the same way as a scale matrix produces new scales. The total number of teeth produced by one tooth matrix is distinguished as a "tooth-family" of which each member is a "tooth-generation." A tooth is always

[1] M. W. Woerdeman. "Beitrage zur Entwichlungsgeschichte von Zahnen und Gebiss der Reptilien. *Archiv fur mikroskopische Anatomie.* Vol. 92.

pushed out by the next succeeding generation of its own family and the two teeth are so related to one another as to be regarded as an older and a younger brother. Further, it is obvious that exostichical and endostichical tooth-families must exist in the reptile and that an exostichical tooth is only replaced by an exostichical and an endostichical tooth by an endostichical. In mammals tooth replacement is of an entirely different character.

I have defined the functional dentition of reptiles as "isocrasic," which means that the exostichical and endostichical teeth are disposed in regular alternation. How this came about has already been described; the components of the endostichos filling up the gaps left between the teeth of the exostichos. Although the characteristics of the teeth themselves do not indicate the composite nature of the dentition, yet this is not infrequently demonstrated by the peculiar way in which the teeth are renewed, viz. alternately. Very striking testimony of alternate replacement is afforded by fig. 97 (fourth essay) in which the premaxillary dentition of a full-grown *Tupinambis nigropunctatus* is represented. This dentition consists of a median tooth and five teeth on either side of the median line. On each side the successional teeth of the first, third and fifth teeth, which are on the point of corroding the fangs of their predecessors, may be seen, but of the succeeding generations following the second and fourth teeth, there is as yet no sign. This is obviously a very efficient manner of renewing the dentition and is a consequence of its distichical nature. The first teeth of the exostichos have been shown to be somewhat older than those of the endostichos. This difference is perpetuated, with the result that a new generation of the endostichical teeth will always appear somewhat later than that of the exostichical teeth. The replacement of the two types of teeth cannot therefore occur simultaneously.

In proof of this alternating tooth change I may draw attention to another fact. The process of tooth replacement is not equally intense in all reptiles. In some animals where the intervals between two tooth-generations is very short, the tooth matrices produce tooth-families rich in generations. In other animals the interval is very long and the tooth-families are poor in generations. As examples of the first type Lacerta and Mabuya may be mentioned, and of the second the genus Calotes. In a somewhat older embryo of the first type three or four generations in different degrees of development exist simultaneously. A horizontal section through the jaw of such an embryo demonstrates clearly that the components of one of the odontostichi are in a more advanced stage than those of the other, and that the tooth change must necessarily take place alternately.

In fig. 113, a section of one half of the upper jaw of an embryo of Mabuya is delineated. The maxilla (black) is cut through lengthwise and sections of the teeth are to be seen between this bone and the toothband (stippled). Close to the maxilla extends a row of five teeth, while on the lingual side of each of these teeth is its successional tooth, still in connection with the toothband. These rows represent the first and second generations of the exostichical

tooth-families. In the interspaces between the pairs of exostichical teeth are sections of endostichical teeth still partially connected with the toothband, and the replacing teeth of which have not yet appeared.

As a result of this condition of the dentition it is obvious that the replacement of the exostichical teeth must be accomplished before that of the endostichical has commenced, for the second generation of the former has already attained a rather advanced stage of development, while there is no vestige of the replacing teeth of the endostichical set. A similar condition is shown in fig. 114, which represents the front part of the upper jaw (maxilla and premaxilla) of a Lacerta. This embryo was somewhat older than that of Mabuya, since the more buccal row of teeth have already coalesced with the skeleton of the jaw. The coalesced teeth represent the first generation of the exostichos. Two such teeth are united with the premaxilla and the two alternating endo-

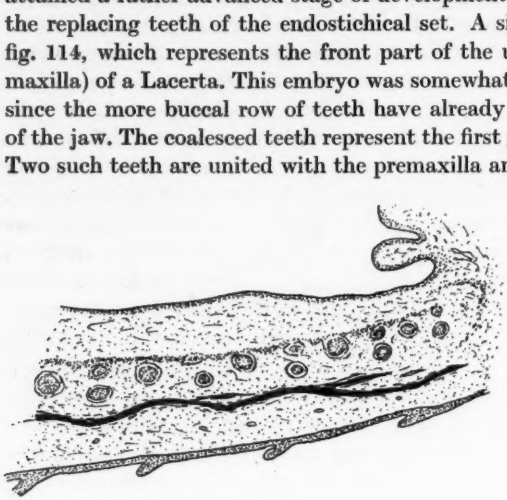

Fig. 113.

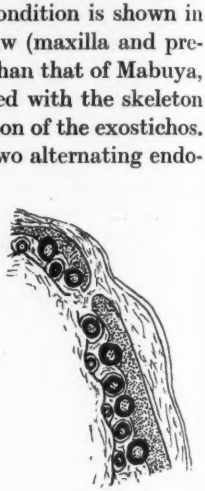

Fig. 114.

stichical teeth are still in connection with the toothband. Three teeth are united with the maxilla and their replacing successors (the second exostichical generation) are present. The three endostichical teeth on the other hand, although occupying the interspaces between the teeth of the first generation of the exostichos, are not yet attached to the bone. This figure illustrates the fact that as a result of the exostichical teeth being formed before the endostichical, the first generation of the exostichos attains attachment to the bones of the jaw before that of the endostichos. This figure also illustrates the way in which the endostichical teeth are intercalated between the exostichical.

The fundamental characteristic of tooth change in reptiles is that each tooth matrix produces a tooth-family, and an older member or generation of this family is continually being replaced by a succeeding or younger member. This modus of tooth change may be termed "merobolic."

The modus of tooth change in the mammal may now be examined and compared with that in the reptile.

Stress has been laid upon the fact that the dentition of reptiles is distichical, the tooth matrices being arranged in two rows. Now the fundamental point to be noticed is, that in mammals a comparable arrangement is found as the

tooth matrices are arranged in two rows the components of which alternate with one another. In mammals, however, the two rows attain a much greater independence, the row which I have distinguished as the exostichos producing the milk teeth, while the second row or endostichos is responsible for the so-called permanent teeth. That the germs of the permanent teeth and those of the milk teeth alternate is a fact which has been recognised for a very long time. This condition is inherited by the mammals from the reptiles in which it is much more evident. Another point of agreement between the two groups of vertebrates lies in the fact that in reptiles the exostichos appears before the endostichos although the interval between them is very short, while in mammals the germs of the exostichical teeth (milk teeth) also appear before those of the endostichical teeth (permanent teeth), but the interval between them is considerably longer. The reason for the retardation of the endostichos is comprehensible as the milk teeth function for a comparatively long period. In many cases, as in man for instance, this period is so long that it is difficult to understand why the germs of the permanent teeth should appear so early in the embryo. This fact, however, becomes intelligible if it is remembered that in reptiles the teeth of the endostichos participate at one and the same time with those of the exostichos in the construction of the functional dentition, and a nearly simultaneous appearance of the teeth of both rows is a necessity. The mammals have inherited the potentiality of a hamastichical dentition from their reptilian ancestors, and although the interval between the appearances of the two sets of teeth is prolonged yet the two sets of germs both appear early.

Having traced the fundamental harmony existent between the dentitions of the reptiles and the mammals, points of difference between the two may now be considered.

As they grow towards the surface the endostichical teeth of the reptile become sandwiched in between the elements of the exostichical row to form with them a single row of teeth. In mammals, on the contrary, the exostichical teeth (milk-set) after becoming implanted into the bones of the jaws, form a continuous series which is retained for a longer or shorter period. In some animals they are absorbed before birth, in others they persist until the animal is full grown. During this period the endostichical teeth (or permanent teeth) undergo further development but remain hidden under the gums until the succession of teeth begins. Consequently the essential character of the mammalian dentition is that the two rows of teeth are functionally independent. The functional dentition consists either of teeth belonging to the first row or of those belonging to the second, both rows functioning successively and not simultaneously as is the case in the reptiles. In contradistinction to the hamastichic dentition of reptiles I term the dentition of mammals "chorisstichic." When the mammal attains the age when teeth-succession occurs an element of the milk-set (an exostichical tooth) is replaced by one of the permanent set (endostichical tooth). The fundamental difference between tooth-

succession in mammals and reptiles can now be defined. In reptiles a tooth is replaced by the succeeding generation of the tooth-family produced by the matrix from which the first tooth was derived (merobolic tooth-change). This process may be repeated as often as the matrix is capable of forming a new member of the family and is practically unlimited. In mammals, on the contrary, a tooth of the exostichos is replaced by one of the endostichos and since the activity of the tooth matrices is condensed into a single production, the whole tooth-family being concentrated into one complicated tooth (*vide* Essay IV) tooth change can only occur in this group but once. In mammals tooth change is a succession of one tooth row after another: in reptiles it is a succession of tooth-generations. The two processes though apparently identical are fundamentally different. In contradistinction to the process in reptiles, which I distinguished as "merobolic," I will denominate that in mammals as "stichobolic."

My contention that, to derive the diphyodontism of mammals from the polyphyodontism of reptiles is a scientific mistake, can now be appreciated, as the difference between the two is not one of quantity but one of quality. In order to render my views intelligible, I have devised two schemes (fig. 115) illustrating the mode of tooth-succession in reptiles and mammals respectively. In scheme "*a*" six tooth-families of a reptile are represented, three belonging to the exostichos (white) and three to the endostichos (striped), four generations of each family being present. The modus of tooth succession is indicated by arrows. In scheme "*b*" the replacement of teeth in mammals is represented, three exostichical teeth (white) and three endostichical teeth (striped) are sketched. The modus of replacement is again indicated by arrows. The two schemes require no further explanation, as they illustrate very clearly the difference between the merobolic succession of reptiles and the stichobolic succession of mammals.

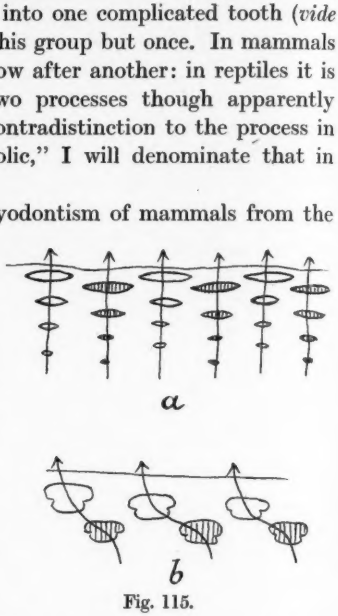

Fig. 115.

Scheme "*b*" presents the view regarding the origin of mammalian teeth which I expounded in my fourth essay and thus the two great odontological problems: (1) the origin of the composite mammalian tooth and (2) the true interpretation of tooth replacement in mammals are brought into line with one another. The two problems have the closest bearing one upon the other, since my theory as to the manner in which the composite tooth of mammals has arisen is incompatible with the view that tooth replacement is comparable with that which occurs in reptiles. In reptiles tooth-succession consists in the replacement of an older generation of the tooth-family by a younger. In mammals the whole tooth-family being concentrated into a single composite

tooth, an entirely new form of tooth-succession must have been acquired. The close correlation between tooth-origin and tooth-succession in mammals is responsible for the plea I advanced in my fourth essay, that criticism of my theory concerning tooth-origin be suspended until my views on tooth-succession had been formulated.

In that essay I defined what I understand by a tooth matrix. In both reptiles and mammals the tooth matrices are arranged in two rows, the components of which exhibit a regular alternation. In reptiles a matrix first produces a tooth, after a shorter or longer interval a second tooth, then a third and so on. During the lifetime of the animal the matrix produces a tooth-family of more or less abundant individuals, an older generation being successively replaced by a younger. This is possible because the members of the family are to all intents and purposes independent of one another and possess a simple form. In the mammals the productivity of the tooth matrix is limited to two generations, owing to the process which I have described in the foregoing essay as tooth concentration whereby the two generations coalesce, the result being a tooth of complicated form (dimer). Thus, the so-called polyphyodontism of reptiles is condensed into the complicated tooth form of the mammals and the diphyodontism of mammals is necessarily a phenomenon of an entirely different nature. I would further emphasise that owing to the structural principle of the dentition inherited by the mammals from their reptilian ancestors, namely, the distichical arrangement, the acquirement of the new modus of tooth change in mammals was rendered possible.

I submit that my theory marks an advance in the morphological understanding of the teeth, as it brings the two principal problems of odontology into logical sequence one with the other and their solution is attained on one common basis.

From the point of view of my theory the doctrine of prelacteal and post permanent dentitions falls to the ground, as it is incompatible with my conceptions. The possibility of such dentitions can only be allowed if the diphyodontism of mammals be regarded as a process identical in nature with the polyphyodontism of reptiles, the difference between the two being purely quantitative. In such case it is justifiable to enquire whether or no there are traces in mammals of tooth-succession preceding or succeeding the two normal dentitions. As according to my theory, the process of tooth-succession in mammals is fundamentally different from that in reptiles, the replacement of teeth being due to a succession of rows, and further, as there are only two such rows (exostichos and endostichos) tooth-succession can only occur once and the possibility of prelacteal or post permanent dentitions falls outside the range of discussion.

Many appearances regarded as traces of a prelacteal or a post permanent dentition have been described and naturally require some explanation. In my second and third essays certain phenomena which I had observed during

my investigation upon the development of the mammalian teeth were described. In order to avoid recapitulation I may here state briefly that the whole complex of phenomena described and interpreted in mammals as traces of a prelacteal dentition are in reality either rudiments of the tooth gland-lamina of reptiles (Essay III) or fragments of the lateral enamel-band of mammals (Essay II). If the significance of these formations had been more generally appreciated the doctrine of a prelacteal dentition would never have attained the importance it has in odontological literature.

As concerns a supposed post permanent dentition I will confine myself at present to a simple denial of its possibility. Some investigators consider the so-called free-border of the dental lamina indicates a post permanent or third dentition. I am convinced that this is an error, but I will reserve its discussion for my next essay where its true nature will be demonstrated and it will become evident that my opinion coincides to some considerable extent with that advanced by Wilson and Hill in their investigation upon the dentition of Perameles[1].

The great importance of the distichical nature of the dentitions both of reptiles and of mammals and of their relationships one to the other has, I trust, been adequately demonstrated. The way in which distichy had origin may now be discussed. The question resolves itself into whether the distichical character of the dentition was acquired by the reptiles as a group or was inherited by them from still more primitive ancestors. An examination of the dentitions of the Selachii not only makes the structure of the reptilian dentition intelligible, but also throws light upon the true nature of the dental lamina in the higher vertebrates. Two views regarding the development of the dentitions of the Selachii have been promulgated. The older, and in my opinion the correct view, is that of Owen, the other is advanced by Hertwig. It is a matter of regret that, considering they have not been substantiated by research, the views of the latter author meet with such general acceptance. As a consequence the real nature of the dental lamina has remained unrecognised ever since Hertwig bestowed upon it the most inappropriate name of "successional-band" (Ersatzleiste).

In Tome I of his *Odontography*, Owen states that the successional teeth of Plagiostoma are situated on the inner side of the jaw and are protected by a mucous fold. According to his opinion these teeth arise from free papillae occupying a furrow in the mucous membrane of the mouth and are not enclosed by an enamel-organ. The lingual wall of this furrow has the character of a "thecal lamina" and the epithelium of the inner surface of this covering fold is continued at the bottom of the groove into the tooth-forming epithelium of the outer wall. "The anterior lamina of this fold which from its office may be termed 'thecal' is continuous with the mucous membrane at the base of the rows of teeth" (*l.c.* p. 35).

[1] J. T. Wilson and J. P. Hill. "Observations on the Development and Succession of the Teeth in Perameles." *Quart. Journ. of Microsc. Sc.* Vol. XXXIX. 1897.

The essential feature of Owen's view is, that the teeth develop upon free papillae which being practically situated on the surface are protected by an overlapping fold of mucous membrane. If this fold be retracted it is at once apparent that the teeth are really situated on the surface. Hertwig's conception, on the other hand, is that a solid band grows from the surface epithelium into the subjacent mesenchyme and that the teeth are formed on the free border of this band. Hertwig asseverates that the mucous fold of Owen is an artefact invented by him in consequence of his researches being limited to the younger teeth. Hertwig's assertion is, without any reasonable doubt, fallacious and I am convinced by the results of my own investigations that Owen is right as the following summary of the phylogeny of the toothb

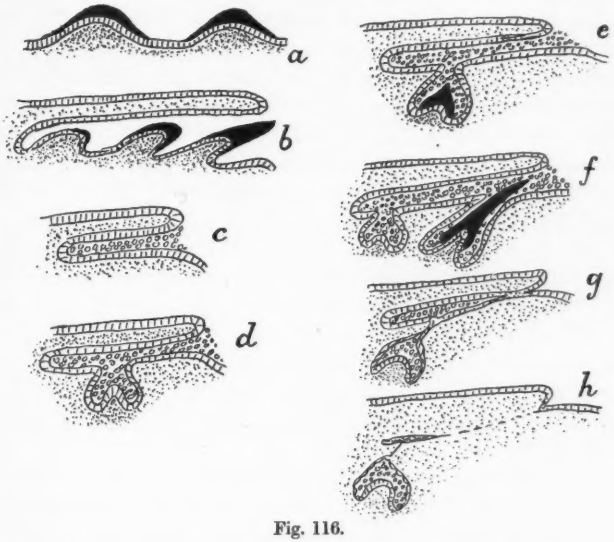

Fig. 116.

will show. The developmental scheme is illustrated by the diagrams in fig. 116.

That the teeth of Selachii are to be regarded as highly specialised dermal denticles is a generally accepted view. These denticles, the so-called placoid scales, are epithelial formations arising upon free papillae. In the first diagram of fig. 116 the position of such scales is represented. In rays and some sharks the relationship between scales and teeth is easily ascertained since there is a direct continuity between the two at the borders of the jaws, the former gradually merging into the latter. Fig. 117 shows another example of this relationship. It represents a part of the dentition of a *Selache maxima*. In this shark the dentition consists of very small teeth definitely situated on the surface and investing the borders of

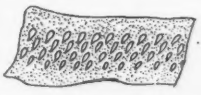

Fig. 117.

the jaws. These teeth and the dermal denticles of the shark are practically identical in structure.

A further phase of development found in the majority of other sharks is shown by the second diagram of fig. 116. In Selache the whole complex of teeth is exposed on the surface; but in other sharks the young teeth are protected by a mucous fold derived from the lining membrane of the mouth. This fold covers the developing teeth and I shall therefore term it the "Operculum dentium" or, in short, the "operculum," while the region of the surface membrane from which the teeth are derived will be distinguished as the "toothfield." The difference between rays and the majority of the sharks is that in the former the toothfield lies freely exposed on the surface being visible for its whole extent, while in the latter, on the contrary, the toothfield, with the exception of a narrow zone bearing the teeth actually functionating, is covered over. Nevertheless in the latter the teeth are to all intents and purposes situated on free papillae of the surface as is the case in the rays, since the deep surface of the operculum is not adherent to the toothfield from which it may be easily retracted thereby fully exposing the complex of developing teeth. It must be obvious to the reader that the formation which I distinguish as the "Operculum" is identical with the "Thecal fold" of Owen and that my conception of the anatomy of the Selachian dentition agrees, as far as this feature is concerned, with that advanced by him.

Another fact to which I would draw attention, as it indicates an important advance in the development of vertebrate dentition, is that in sharks the origin of the teeth is not autonomous. This is demonstrated by fig. 116 *b*, where a furrow is to be observed between the operculum and the toothfield. At the bottom of this furrow the epithelium on the deep aspect of the operculum becomes continuous with the epithelium of the toothfield. The matrices responsible for the production of the teeth are disposed along this line of epithelial reflexion. As a tooth enlarges it migrates towards the border of the jaw, and after a longer or shorter pause, the matrix from which it was derived produces a second tooth, and so on. In fig. 116 *b*, three tooth generations all derived from the same matrix and exhibiting progressive stages of development are shown. The totality of all the teeth having origin from one and the same matrix I have previously termed a tooth-family. In sharks a number of generations or members of such a family are always found under cover of the operculum.

Sharks often furnish very conclusive evidence of my contention that the teeth of the vertebrates are not autonomously arising organs but are produced from a matrix. Disposed between tooth-families whose members are normal in shape a family of teeth exhibiting some anomalous form may appear. Fig. 118 represents the mandibular dentition of a young Spinax niger, with five tooth-families, each consisting of four generations at least. The teeth are tricuspidate with a long sharp central cusp on either side of which are two smaller cusps. In addition to the families all the teeth of which are normal, there is one

family whose members without exception present a duplicated main or central cusp. Such a phenomenon is unintelligible unless it be conceded that all these anomalous teeth are produced from one and the same matrix, which for some reason or another, must have undergone some modification in structure and function.

Another case illustrating a similar condition is given in fig. 119, which represents a part of the dentition of *Cephaloptera giorna*. The teeth of this shark are very small and the sharp extended edge of each tooth is serrated exhibiting five little cusps. Between the normal families is one whose members are double the length of and are provided with twice as many cusps as the normal tooth. I am quite convinced that if the dentitions of a great number of sharks were examined examples of similar cases would be easily found. Such cases leave little room for doubt that in sharks—and consequently in reptiles also—the teeth are derived from special matrices.

With this digression the developmental history of the toothband may now be further considered. In fig. 116 *c* a further stage of development is repre-

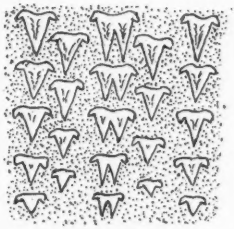

Fig. 118.

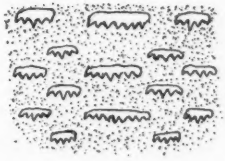

Fig. 119.

sented. The toothfield and the operculum may still be recognised. If it be compared with fig. 116 *b* it will be noticed that it has progressed in so far that the furrow between the operculum and the toothfield is now filled up with cells forming a connecting medium between the two.

In this stage a real toothband consisting of two epithelial layers separated from one another by a layer of indifferent cells may be described. The two epithelial laminae however, are far from being equivalent, as one, homologous with the toothfield of sharks, is alone concerned in the production of teeth, while the other which represents the lining epithelium of the operculum is inactive as far as tooth formation is concerned.

Figs. 116 *d*, 116 *e*, and 116 *f*, represent three stages of tooth development in reptiles. The toothband is again composed of two epithelial laminae; the toothfield-lamina and the operculum lamina which are attached to one another by an intermediate layer of indifferent cells. The toothgerms are formed exclusively from the toothfield-lamina, and the enamel-organ is in direct communication with the layer of indifferent cells filling up the interior of the enamel-organ, where they are differentiated into the well-known reticulum or enamel-pulp.

As soon as the hard tissue of the tooth is sufficiently developed, the tooth begins to push its way between the two laminae of the toothband, as is shown in figs. 116 *e*, and 116 *f*. A comparison of the figs. 116 *b*, and 116 *f*, shows the fundamental agreement between the dentitions of sharks and reptiles. In the reptile, however, the real toothband has appeared as a result of the fusion of the operculum and the toothfield, the latter sinking to a certain extent into the underlying tissue.

The open enamel-organ together with a continuity between the enamel-pulp cells and the cells of the intermediate layer of the toothband are characteristic of a great number of reptiles, in which the enamel-organ never loses its connexion with the dental lamina. Nevertheless, in one group of these vertebrates, viz. the Crocodilia, evolution as concerns both the toothband and the enamel-organ is markedly progressive. In these animals, as may be seen in fig. 116 *g*, the layer of intermediate indifferent cells is not well developed in the toothband in which the operculum and toothfield epithelial layers are, more especially near the surface, in close proximity with one another. Not infrequently the continuity of the toothband with the superficial epithelium is actually interrupted. This occurs in older embryos in which, as a consequence, the toothband is isolated from the surface and is buried in the mesenchymatous tissue. In this respect the crocodiles approach the evolutionary stage peculiar to mammals. The two groups of vertebrates are also alike as regards the enamel-organ. In lower reptiles this organ is in close connexion with the epithelial lamina of the toothband, identical with the toothfield epithelium of sharks. In crocodiles the attachment of the toothgerm to the toothband diminishes and the enamel-organ becoming more and more independent is eventually connected to the toothband by a narrow strand of cells. Finally the enamel-organ is detached from the band and becomes completely surrounded by mesenchymatous tissue, some isolated patches of epithelial cells between the band and the organ testifying to the original continuity of the two.

Setting aside these more advanced stages of evolution by which the crocodiles approach the mammalian conditions, stress must be laid upon the fact that in crocodiles the enamel-organ is produced exclusively by that component of the toothband which is identical with the epithelium of the toothfield in fishes while the component corresponding to the original lining epithelium of the operculum takes no part in the formation of the toothgerms.

The conditions met with in crocodiles enable us to understand those in mammals. In the latter group, the toothgerms are also produced by the epithelium corresponding to the original toothfield, being always formed upon the outer or labial aspect of the toothband. In reptiles the toothband becomes detached from the superficial epithelial layer more completely and at an earlier stage; further, early and complete detachment of the toothgerm from the toothband also applies. Very young embryos of some mammals demonstrate very clearly the primitive structure of the toothband consisting, as it

does, of an inner lamina (the primitive opercular epithelium) and an outer lamina (the primitive toothfield epithelium), a layer of indifferent cells intervening between the two. In some cases I have observed a characteristic difference in shape of the cells of the two laminae, those of the inner lamina being more flattened as compared with those of the outer. However, these primitive features commonly disappear very early.

This summary establishes the view that the phylogenetic history of the toothband is in reality very simple, and that a true conception of the real nature of this band is only possible after a survey of all the phylogenetic facts. The evolution of this band commences with the overlapping of the toothfield by the operculum in sharks. The ontogeny of mammalian dentition is based upon this phylogenetic process although its earliest stages cannot be observed. This primitive phylogenetic stage is often discernible however, in reptilian embryos as is demonstrated in figs. 120 and 121. In fig. 120 a section is drawn through the third tooth of the upper jaw of a young embryo of *Gongylus ocellatus*. A true toothband is not yet formed, but a broad shallow furrow filled up with intermediate cells is present. On the buccal side of the furrow a papilla arises and its similarity to the free papillae of the early dentition of

Fig. 120.

Fig. 121

sharks is very obvious (cf. fig. 116 *b*). Fig. 121 represents a section through the same tooth of a somewhat older embryo, and in this the formation of the hard tissue has commenced. It shows very clearly that the mucous membrane lining the mouth is disposed in the form of a fold which is beginning to overlap the young tooth. This fold is obviously the operculum.

The phylogenetic history of the toothband teaches us that its denomination by Hertwig as "successional band" (Ersatzleiste) is quite incorrect since the band had origin, not as an ingrowth of the superficial epithelium into the subjacent tissue, but as a result of the overlapping of the teeth-forming zone by a fold of mucous membrane. Tooth-succession is not associated with the band in its entirety, but only with one of its components, namely with that correspondent to the epithelium of the primitive toothfield. The true character of the band is only intelligible if it is considered as a result of a process of opercular formation.

Having established the phylogeny of the toothband, the question as to the origin of the peculiar construction of the reptilian dentition can now be discussed. A fundamental feature of the dentition is the fact that the first reptilian teeth are arranged in two rows or odontostichi on the buccal side of

the dental lamina, and that the elements of the two rows alternate with one another. This condition I distinguished as distichy. Assuming that the buccal lamina of the reptilian toothband is identical with the toothfield of the sharks, an idea as to the manner in which this distichy came about can be conceived. In order to do this the structure of the selachian dentition must be carefully examined.

Fig. 122 represents a part of the mandible of a *Carcharias glaucus*, as seen from the outer side. If the arrangement of the functional teeth set upon the

Fig. 122.

border of the jaw be examined, it is obvious that they are disposed in two rows, an outer and an inner, the components of the two rows exhibiting a regular alternation. The similarity of the arrangement to the reptilian dentition is very striking, since the latter is built up from two rows of teeth derived respectively from endostichical and exostichical teeth matrices. There is however one important difference. The primitive distichical character of the functional teeth in reptiles is obscured in that the teeth of the inner row are intercalated regularly between those of the outer row. In Carcharias on the contrary and apparently in other sharks as well, this intercalation does not take place and the distichical character is manifest.

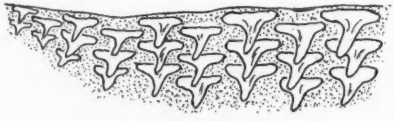

Fig. 123.

By examining the inner side of the jaw, where the replacing teeth are still lying recumbent, it is evident that this distichical arrangement of the functional dentitions will persist. In fig. 123 a part of this dentition exposed by removing the operculum is sketched. As in reptiles it consists of a number of tooth-families there being no difference between the construction of the selachian dentition and that of reptiles. The existing members of each selachian tooth-family may however be more numerous than those in reptiles. This circumstance is due to the fact that in sharks the process of tooth change has greater intensity than that in reptiles. I would draw special attention to the alternating positions of the members of the tooth-families.

Not only does the construction of the reptilian dentition agree with that of sharks, but the factor determining distichical arrangement of the former can be appreciated if it is realised that the selachian dentition is so arranged in parallel rows that the component elements of one row alternate with those in an adjoining row.

Consequently the distichical character of the dentitions of mammals and reptiles is inherited from very primitive ancestors, in which it was simply a retention of an arrangement characteristic of the skin investment of the animal. In reviewing all these facts and keeping especially in mind that tooth change in mammals is a succession of tooth rows (and not, as in reptiles, a succession of tooth-generations) the following somewhat surprising conclusion can be drawn. *The modus of tooth change in mammals is based upon the arrangement of the dermal denticles of the skin in primitive vertebrates.*

A FOETUS PRESENTING A COMBINATION OF RARE ANOMALIES

By H. A. HARRIS

Ernest Hart Memorial Scholar, B.M.A. Dept. of Anatomy, University College, London

The investigation of the interdependence of the various processes of growth is attracting less attention than the search for evidence of the interdependence of the various physiological processes in the circulatory, excretory and endocrine systems. It therefore seems advisable to analyse all monsters with a view to ascertaining the extent of "action at a distance" in the various processes of growth. This attitude is the justification for the following description of a male foetus miscarried in the twenty-seventh week of pregnancy by a primiparous woman of 25 years of age. The foetus presented as a breech in the unruptured bag of membranes. The placenta was retained for one hour and its separation was followed by a sharp post-partum haemorrhage. The general health of the mother was good before and during pregnancy, and there was no history of a previous miscarriage. The paternal and family histories yielded nothing of note.

External Features

The foetus had been dead for some days *in utero*, and its macerated condition unfortunately interfered with histological examination. The length from crown to rump is 16 cms., and the weight is 400 grams. The subcutaneous fat and muscles are badly developed and the left half of the thorax appears to be markedly collapsed. The umbilical cord displays but one artery and one vein, a condition which is usually associated with some degree of sympodia (Ballantyne '04, Dawson '22), but which, in this case is associated with a right club-foot. The left arm is very short and presents only two fingers. The head and its apertures appear normal, but there is no trace of the anus or post-anal dimple, the median raphe extending from the tip of the coccyx to the base of the penis, which, with the scrotum, is normally developed for seven months.

X-Ray Examination

The vertebral column is decidedly irregular (fig. 1), the marked scoliosis being accompanied by malformation of the eighth and ninth dorsal vertebrae, which are wedge-shaped and exhibit single asymmetric centres of ossification for the centra. The upper seven dorsal vertebrae present double centres symmetrically placed and the third sacral presents a single asymmetric centre. The centres of ossification for the neurocentral arches are normal except in

the case of the eighth and ninth left dorsal arches, where they are suppressed, and the sixth and seventh left, where they are fused. The ribs on the right side are normal, but on the left side the eighth and ninth ribs are wanting,

Fig. 1. Radiogram of the Foetus.

and a first lumbar rib is present; moreover, varying degrees of fusion have occurred between the third, fourth, and fifth, the sixth and seventh, the eleventh and twelfth, so that posteriorly the eleven ribs are distributed over thirteen vertebrae, whereas anteriorly the number is apparently reduced to

eight ribs, the first to the seventh being vertebro-sternal, the tenth to the twelfth vertebro-costal, and the thirteenth floating. The sternum displays centres of ossification in the three upper segments, a degree of ossification which is normal for the seventh month of foetal life.

The left upper limb has a short humerus, no radius or ulna, and two metacarpals with three phalanges apiece. There is a trace of a more radial metacarpal, but no phalanges are attached thereto. The centre of ossification for the body of the pubis has not appeared and the right foot is clubbed, the deformity being concentrated at the neck of the astragalus. The centre of ossification for the os calcis is present.

A. The Vertebral Column and Ribs

Ossification normally commences in the neuro-central arches (hemi-arches) of the cervical vertebrae about the seventh week of foetal life, and, extending caudally, reaches the region of the third sacral vertebrae about the seventh month. Ossification commences in the centra of the lower dorsal region about the seventh week, and, extending cranially and caudally, reaches the odontoid process at the fourth month and the fifth sacral vertebra at the fifth month. In the ribs, ossification takes place a few days ahead of ossification in the vertebrae, commencing in the seventh rib and spreading cranially and caudally (Pinkus '10, Keith '21). The extent of the anomalous development in the vertebrae and ribs of this foetus is shown in the radiogram (fig. 1) and in the diagram constructed therefrom after dissection of the vertebral column (fig. 2). Perhaps the most interesting feature is the condition presented by the eighth and ninth thoracic vertebrae, in which the left half of the vertebrae is suppressed.

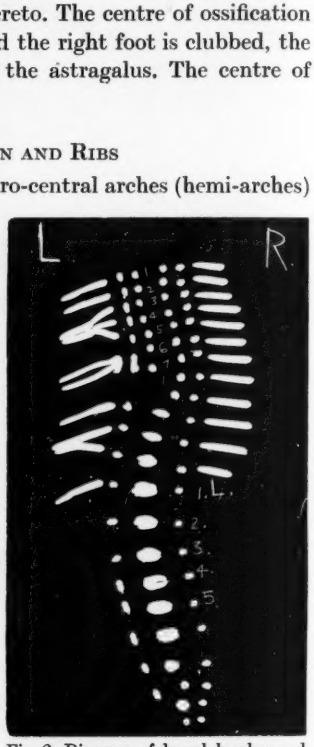

Fig. 2. Diagram of dorsal, lumbar and sacral portions of vertebral column.

The first record of deficiency of a half vertebra appears to be that of Rokitansky (1842), who regards the deficiency as a well-recognised cause of scoliosis. On the other hand, Struthers, in his description of vertebral variations (1875) does not mention absence of half a vertebra. In the same year Goodhart reports cases of deficiency of a half vertebra and cases of "doubling" of the centrum. Brash (1914–15) gives a summary of the literature previous to and after the advent of X-ray diagnosis and points out that there is a dearth of post-mortem corroboration of those cases of scoliosis which have been attributed to this cause. The most comprehensive studies of the anomalies of the vertebral column are those of Joachimstal ('10) and Falk ('20).

In the recorded cases of vertebral anomalies there are but few references to the ribs. Goodhart (1875) records the case of an adult with the whole of the first lumbar, the left half of the twelfth thoracic, and the right half of the second lumbar vertebrae wanting, with the existence of a thirteenth rib on the left side. Willet and Walsham (1880) record a case of deficiency of four and a half vertebrae in the upper dorsal region, the fourth left and fifth right ribs being wanting. Bolk has described a human skeleton showing bifurcation of several ribs and a number of small bones intercalated between the laminae in the dorsal region of the spine. Falk (1920) describes several cases of deformities of the ribs associated with malformation of the vertebral column and quotes Putti as follows:—"Since the rib is to be regarded as a product of the ventral portion of the hemi-arch, the costal anomaly of the thoracic skeleton is always inseparably bound up with a vertebral anomaly, so that in a lack of the costal element, either a half vertebra or at least the ventral portion of the hemi-arch is missing. Also in fusion of the ribs, a sign of irregular segmentation exists in the vertebra."

An analysis of the cases of suppression or intercalation of a half vertebra shows that there is a site of maximum frequency. The condition has been observed from the third cervical to the third sacral region, fifty per cent. of the cases occurring between the eighth dorsal and first lumbar. As regards doubling of the centres, this is still more marked, as ninety per cent. of the cases occur between the first and ninth dorsal vertebrae. Ever since von Baer (1837) called attention to the asymmetry of the embryonic axis in relation to the yolk sac, various mechanical factors with marked bending, wrinkling or torsion of the embryonic axis have been invoked to explain skeletal anomalies. Jansen ('21) maintains that the stress of increased amniotic pressure in the precartilaginous (sclero-blastemous) stage of the embryo, when the amnion lies dorsal thereto, falls on the cervical and lumbar regions, leading to anencephaly and spina bifida. During the early cartilaginous stage when the amnion surrounds the embryo, the stress falls on the head, lumbo-dorsal column, and extremities, leading to achondroplasia (Jansen) and mongoloid idiocy (Van der Scheer '18). Brash ('14–'15) records the case of a man with an absent half vertebra who served in the army and was free from marked deformity. The protagonists of excessive amniotic pressure have not described frequent vertebral anomalies, other than kyphosis in the cases of achondroplasia and mongoloid idiocy. Thus the limitations of the mechanical theory are evident.

Falk rejects the various mechanical theories and attributes the condition to a defect of the primitive segmentation. It is evident that the problem must be examined anew in terms of the evolution of skeletal segmentation, and for this reason all cases of vertebral and costal irregularities, especially those ascertained in the course of routine X-ray examination, should be recorded.

B. The Thorax

The thymus is small and fails to cover any portion of the pericardial sac. The heart is displaced to the left and upwards so that the right border lies behind the right half of the sternum and the apex reaches the anterior border of the axilla in the third intercostal space. The pericardium is adherent to the antero-lateral portion of the collapsed thoracic wall up to the level of the second intercostal space. The right lung is normal, but the left lung is absent. There is no trace of a left pleural cavity as the pericardium is loosely adherent to the costal parieties. The dome of the left half of the diaphragm ascends posterior and lateral to the pericardial sac and is closely applied to the postero-lateral aspect of the chest wall to the level of the third rib, loose areolar tissue intervening. The left wall of the pericardial sac contains numerous muscular fibres supplied by twigs from the left phrenic nerve.

The presence of muscular fibres innervated by the phrenic nerve in the left wall of the pericardium, the contiguity of the left half of the diaphragm and the costal parietes up to the level of the third rib space, together with the absence of the left pleural cavity and lung is of great importance in connection with Keith's ('05, '10) description of the rôle played by the rectus abdominis and transversalis sheet of muscle in the formation of the diaphragm. I hope to discuss the significance of the condition here met with in a further contribution dealing with two atypical cases of diaphragmatic hernia.

The oesophagus is definitely interrupted at the level of the seventh cervical vertebra (fig. 3). The larynx and cervical trachea are normal but the bifurcation of the trachea presents a striking anomaly. The right bronchus leads to the right lung, but in place of the left bronchus is a small canal of 1 mm. diameter, lined with epithelium, which passes downwards for 8 mm. to become continuous with the distal portion of the oesophagus at the level of the sixth dorsal vertebra (fig. 3).

Tracheo-oesophageal and broncho-oesophageal fistula with stenosis of the proximal part of the oesophagus has been frequently reported. Comprehensive studies of the condition have been published by Morell Mackenzie (1884), Happich ('05), Forssner ('07), Giffhorn ('08), Phillips ('08) and Keith ('10). Three characteristics are afforded by the cases described; firstly, the large number of associated abnormalities such as imperforate anus, pulmonary stenosis, club foot, spina bifida and right aortic arch; secondly, the limitation of the stenosis of the oesophagus to the site of junction of two morphological portions of the oesophagus, the para-tracheal and retro-tracheal portions of Keith; thirdly, the site of origin of the tracheo-oesophageal fistula from the dorsal wall of the trachea near its bifurcation. Forssner and Keith attribute the condition to the lateral margins of the distal portion of tracheal groove uniting on the dorsal wall of the gut instead of in the ventral wall.

The lung anlage of the 2·5 mm. embryo and of the 4·25 mm. embryo (Rob. Meyer) is definitely unpaired. In the 4·9 mm. embryo (Hertwig) and

5 mm. embryo (Rob. Meyer) the trachea is definitely divided off from the oesophagus and the right and left lung buds are developed; the right lung bud is the larger and is directed caudally, while the left has an almost transverse direction. In the 4 mm. embryo Broman shows in addition to the tracheo-oesophageal septum which is as yet not separated off, a lateral

Fig. 3. Stenosis of the oesophagus with tracheo-oesophageal fistula. *Tr.* trachea; *Oe.* oesophagus; *F.* fistula; *CC.* common carotid; *Ao.* aorta; *S.* subclavian; *V.* vertebral artery.

oesophageal groove which causes the oesophagus to be a narrow antero-posterior figure 8 on cross-section. Obliteration of the posterior lumen of the figure 8, with persistence of the communication between the anterior lumen of the figure 8 and the trachea would lead to the condition which is being discussed. This has been suggested by Lewis ('12).

Keith and Spicer have described three consecutive cases of stenosis of the

oesophagus with persistence of that abnormal right subclavian artery which passes dorsal to the oesophagus, and have attributed some function to this portion of the fourth right dorsal arch in the production of the deformity. This explanation is not warranted, as in the 4 mm. embryo, which is close to the stage at which the deformity must arise, the fourth branchial artery is in relation to its branchial pouch and the dorsal aortae fuse in the neighbourhood of the second cervical segment. Similarly in the case under discussion the position of the tracheo-oesophageal fistula in relation to the left aortic arch (fig. 3) does not exist throughout development, as the elongation of the oesophagus takes place much more rapidly and to a far greater extent than the migration of the arches. The absence of the left bronchus and lung makes this case quite different from any of the fourteen cases collected by Keith ('10) from the Museums of the Royal College of Surgeons and Metropolitan Medical Schools.

C. The Heart and Great Vessels

The apex of the heart is bifid, and the ventricular septum is complete. The walls of the auricles are thin and the auricular septum is deficient, being represented by a few strands of tissue which cross the cavity on the posterior wall. The auriculo-ventricular, aortic, and pulmonary valves are normal. The Eustachian valve guarding the entrance of the inferior vena cava is normal, but the Thebesian valve guarding the entrance of the coronary sinus is larger than normal, the opening of the sinus being larger than the opening for the inferior vena cava. The auricular walls average 0·5 mm. in thickness and the ventricular walls 2·5 mm.

The bifid apex is a condition which may appear with or without grave anomalies, and is normal to the dugong. In the 5 mm. embryo, when the primary auricular and ventricular septa are forming, rapid downgrowth of the apices of the ventricles takes place so that the interventricular groove is distinct. Obliteration of this deep groove takes place in the 11 mm. stage by development downwards of the embryonic apex (Abbott '15). Mall ('12) maintains that persistence of the bifid apex is due to absence of the muscular vortex normally present at the apex. A deeply bifid apex occurred in three of Théremin's 106 cases, and in four of Abbott's 631 cases of abnormal hearts.

The auricular septum in this heart is represented only by a few strands which cross the cavity in the dorsal wall, so that the heart is virtually a case of "cor biventriloculare." It is probable that this is an example of a huge persistent ostium secundum (foramen ovale) which has escaped closure through failure of development of the septum secundum. Such an anomaly is rare and points to the possibility of a disturbance occurring after the appearance of the septum primum (4 mm. stage) and before the appearance of the septum secundum (8 mm. stage).

In a series of 631 cases, Abbott reports 14 cases of rudimentary auricular

septum and five cases of complete absence, and states that persistence of the left superior vena cava belongs to the same complex.

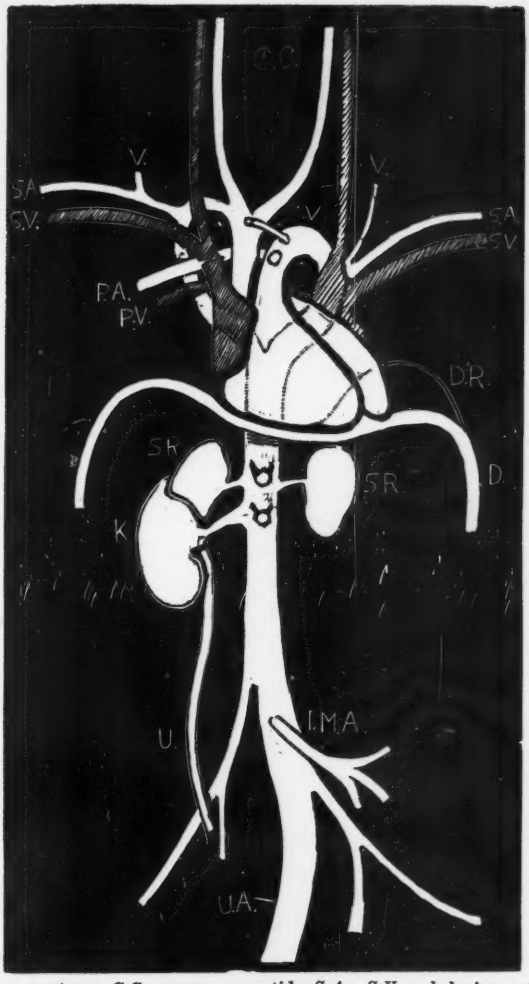

Fig. 4. Circulatory system. *C.C.* common carotid; *S.A.*, *S.V.* subclavian artery and vein; *P.A.*, *P.V.* pulmonary artery and vein; *D.* diaphragm; *D.R.* diaphragmatic recess posterolateral to pericardium; *S.R.* suprarenal; *K.* kidney; *U.* ureter; *U.A.* umbilical artery; *I.M.A.* inferior mesenteric artery; ⊙ recurrent laryngeal nerves; *C.V.* vessel communicating posterior aspect of the two systemic arches. The vessel is shown anteriorly for clearness.

The internal jugular and subclavian veins of the right side form a vena cava superior which enters the right auricle. The corresponding vessels on the left form a vena cava superior which passes anterior to the left systemic

arterial arch to form a dilated coronary sinus which enters the right auricle. The fused pulmonary veins from the right lung enter the left auricle as a single trunk near its upper border. The inferior vena cava and azygos system are normal. The phrenic and vagus nerves are also normal in their course and relations in the neck and thorax.

The anomaly presented by the great veins is due to a persistence of the embryonic left superior vena cava and left duct of Cuvier with consequent replacement of the coronary sinus. This arrangement is normal in many mammals (Robinson '17). The left superior intercostal vein entered the left superior vena cava and the great cardiac vein entered the coronary sinus, but there was no trace of a left vena azygos major, neither was there a left lung root to assist in the task of ascribing any definite rôle to any minute anastomosis. The anastomosis between the left and right superior venae cavae in the neighbourhood of the thymus was not well marked.

The great arteries of the thorax present a condition hitherto undescribed. From the left ventricle (fig. 4) arises a right systemic arch which runs upwards and slightly to the right, arches backwards over the root of the right lung, and gives off in turn the left carotid, right carotid and right subclavian vessels. From the right ventricle ascends a left systemic trunk which is anterior and to the left of the vessel arising from the left ventricle. As it arches upwards and to the left it gives off a right pulmonary artery which passes dorsal to the ascending portion of the right systemic arch; it then continues as a well-defined arch, gives off the left vertebral and left subclavian arteries, and descends to join the right arch to form the descending aorta at the level of the upper border of the fifth dorsal vertebra. The calibre of the left arch is much greater than that of the right arch, and the terminal portion of the left arch lies immediately dorsal to the fistula between the trachea and oesophagus (fig. 3). A small communicating vessel of great interest runs from the posterior aspect of the ascending portion of the right arch to the posterior aspect of the ascending portion of the left arch. The abnormal termination of the abdominal aorta is clearly shown in fig. 4, the inferior mesenteric artery arising as a branch of the single (left) umbilical artery.

Rathke's classical description of the fate of the embryonic aortic arches, as modified by Boas (1887), is shown (fig. 5) for the sake of comparison.

A comparison of fig. 6 with fig. 4 will indicate the nature of the explanation tentatively adduced to elucidate the arrangement of the primitive aortic arches in this foetus. The third arch on each side forms the commencement of the internal carotids. The fourth arch on the right side forms the transverse part of the right systemic arch. The sixth arch on the right persists as far as the outgrowth which forms the right pulmonary artery. The sixth arch on the left persists *in toto* as ductus arteriosus to form the transverse part of the left systemic arch. The small vessel communicating the ascending portions of the two great vessels arising from the heart may be regarded as a persistent fifth left arch, a persistent fourth left arch, or a vessel comparable to the small

artery which is depicted by Tandler ('02), as an "arterien insula" in relation to the aortic arches. The proofs given by Evans ('09) that all the arteries develop originally as well-defined capillary networks permits of a chance

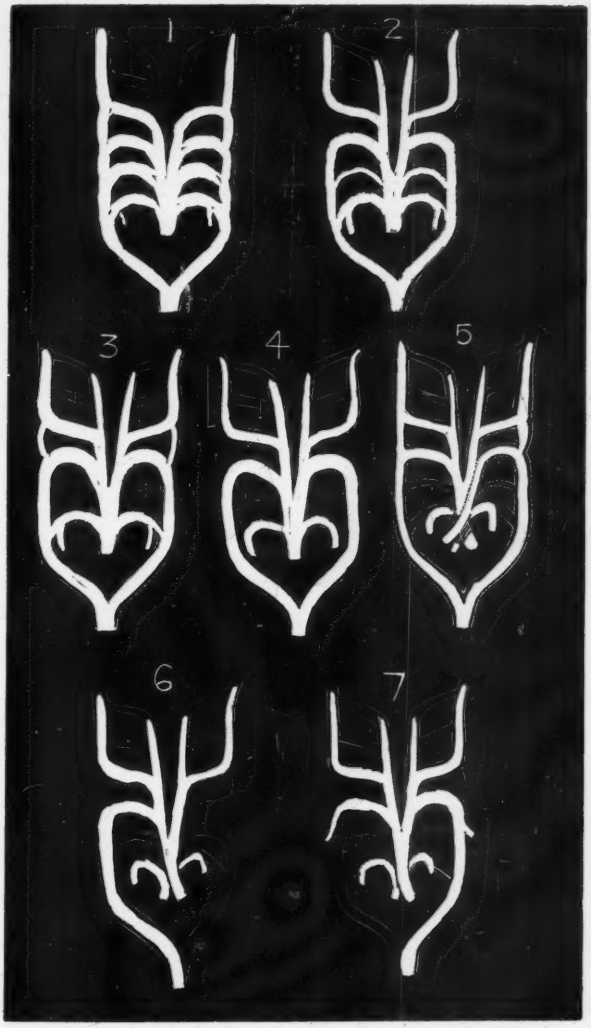

Fig. 5. The aortic arches and their transformations (after Rathke). 1. Ceratodus; 2. Salamander; 3. Triton; 4. Frog; 5. Lizard; 6. Bird; 7. Mammal.

anastomosis persisting along with the definitive arches. Most anatomists would regard this small vessel as a persistent fourth arch because the fifth arch of van Bemmelen (1886) is a transitory structure. Quite as legitimately

one might argue that since the fourth left arch usually persists as the definitive aortic arch, this vessel cannot be the fourth arch. There is no certain means of

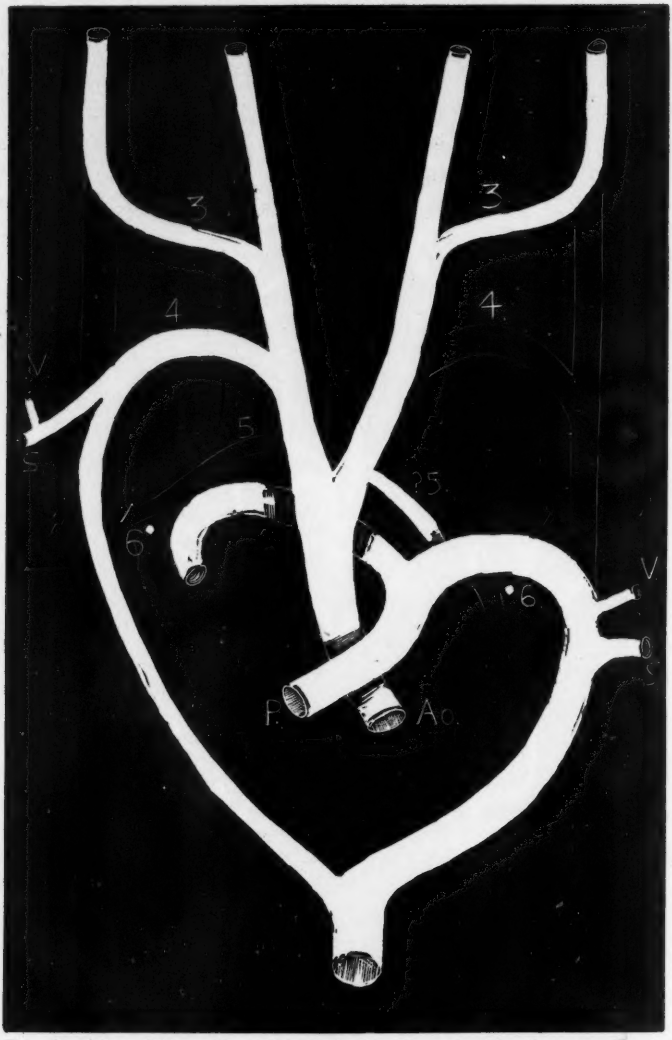

Fig. 6. Transformation of the aortic arches (cf. fig. 4). *Ao.* aorta; *P.* pulmonary; *S.* subclavian; *V.* vertebral; ○ recurrent laryngeal nerves.

ascertaining the identity of this vessel as no trace of the nerve of the fifth arch, the nervus post-trematicus of the superior lanyngeal branch of the vagus (Elze '07) has been recorded in embryos of more than 20 mm.

The work of Bremer ('02, '08) has shown the incorrectness of the conventional diagrams (fig. 5) in which both definitive pulmonary arteries are shown as sharing equally in the proximal parts of the left and right sixth arches, for in no mammal is this true. Man and most of the other mammals have a right pulmonary artery which is of this nature, but the left pulmonary artery is merely the original pulmonary outgrowth of that side, the corresponding proximal portion of its arch having been assimilated in the pulmonary trunk. In this specimen, in accordance with the absence of the left lung there is no trace of the left pulmonary arterial outgrowth from the left sixth arch. The positions of the recurrent laryngeal nerves are shown in fig. 6 and they confirm the tentative explanation of the fate of the aortic arches in this foetus.

The subclavian of the right side is normal and represents the seventh segmental artery with the proximal part of the vertebral as its posterior primary division. The left subclavian artery has not moved cranially so far as the right, so that it retains its attachment to the dorsal aorta in the neighbourhood of the dorsal root of the sixth arch; and the vertebral, by absorption of the proximal part of the seventh segmental artery arises directly from the dorsal root of the sixth arch. This independent origin of the vertebral artery is comparable to the anomalous origin of the vertebral from the arch of the aorta (Thane 1896). Whereas in the latter case the vertebral artery usually enters the foramen transversarium of the fifth cervical instead of the sixth, in this case the vertebral entered the sixth.

The surveys of Tiedemann (1829), Peacock (1866), Turner (1862) and Abbott ('15) provide but few cases in any way comparable to the above, and no identical case has been found in the literature. The cases presenting a resemblance to the one under discussion can be arranged in three groups (Turner 1862):—

1. "Cases presenting atrophy of the fourth left aortic arch between the origins of the common carotid and subclavian arteries, with persistence of the sixth arch."

Greig's (1852) famous case was that of a foetus in which two arteries arose from the base of the heart; one, the aorta, ascended to the right and divided into left common carotid, right common carotid and right subclavian; the other, the pulmonary, gave off a branch to each lung and then continued onwards into the descending aorta which received its supply of blood solely from this source. The left subclavian arose from the latter trunk after it had given off the branches to the two lungs. The ventricular septum was also deficient in its upper part. Breschet reported a case in which the left subclavian arose from the pulmonary artery, but no account is given of the condition of the aorta.

2. "Cases presenting atrophy of the fourth left aortic arch beyond the origin of the subclavian."

This group includes those cases of coarction of the aorta which are divided into two sub-groups:—

(*a*) A diffuse narrowing of the aorta at the isthmus [Bonnet's ('03) infantile type]. In some of these cases in which the stenosis is marked, the circulation in the lower part of the body is maintained by a large patent ductus arteriosus

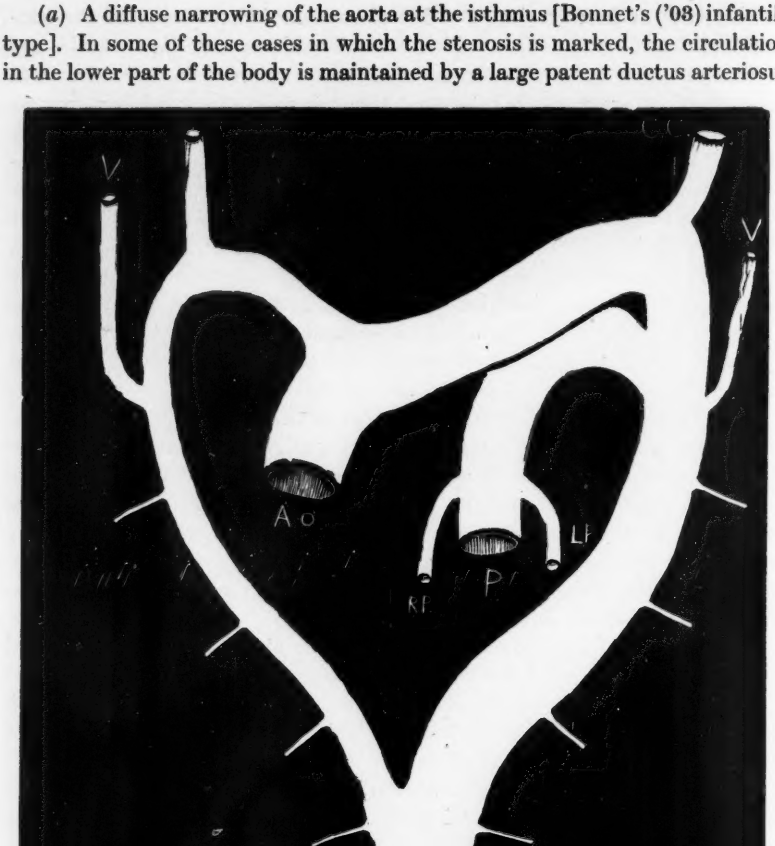

Fig. 7. Aortic system of His' embryo Si. 12·5 mm. *Ao.* aorta; *C.C.* common carotid; *V.* vertebral artery; *P.* pulmonary trunk; *R.P.* and *L.P.* right and left pulmonary arteries.

through which the descending aorta appears to be a direct continuation of the pulmonary artery.

(*b*) A more or less abrupt construction of the aorta at or near the insertion of the ductus arteriosus (Bonnet's adult type). Here, where coarction is marked, and has lasted some time, the establishment of an extensive collateral circulation

lends distinctive features to the case. Amongst 212 cases collected by Peacock, Bonnet and Abbott, fifteen cases were of a marked infantile type so that the descending aorta was supplied by a large patent ductus arteriosus. The first case of complete coarction was that reported by Steidele (1826).

3. "Cases presenting transference of the left subclavian at its origin from the fourth to the sixth aortic arch."

In the case recorded by Holst (1836) the vertebral was given off at the place of junction. A closely similar case was reported by Hildebrand (1842), but the left vertebral arose from the left common carotid.

Thus this particular case is unique in the combination which it presents of a persistent right systemic arch, patent ductus arteriosus with marked coarction of the fourth left arch, and a small communicating vessel of unknown origin. Still further is it complicated by the absence of the left pulmonary artery.

The 12·5 mm. embryo described by His (fig. 7) presents a right arch of small calibre, a fourth left arch of large calibre and a patent ductus. The obliteration of the fourth left arch and of that portion of the dorsal aorta between the dorsal roots of the fourth and sixth arches on this side would give rise to a condition closely resembling that in the foetus described. Moreover, the relative calibre of the right and left systemic arches in this embryo is approximately the same as in the foetus.

D. Abdomen and Pelvis

The anterior abdominal wall is poorly developed. The umbilical vein is normal but the single umbilical artery is disposed to the left, there being no trace of the right umbilical artery to the right of the empty bladder. The viscera are normal in disposition, but the inferior mesenteric artery arises from the left umbilical artery below the bifurcation of the aorta which occurs at the level of the third lumbar vertebra (fig. 4).

The rectum (fig. 8), distended with meconium, reaches to within 1·5 mm. of the surface in the region of the imperforate anus. The viscus presents a well-marked ampulla of 6 mm. diameter which ends by a small canal of less than 1 mm. diameter in a cul-de-sac. There is no fistulous communication between the rectum and the urethra. The main valve of Houston is well-developed at the level of the recto-vesical fold of peritoneum.

The statistics of atresia ani et recti in its various modifications, as collected by Curling (1876), Spriggs ('12) and Keith ('10), show that the commonest anomaly is imperforate anus with recto-urethral fistula opening in the region of the termination of the prostatic urethra. More than 60 per cent. of Keith's male cases fall into this group whereas only seven cases out of 54 present the condition represented in fig. 8, i.e. atresia ani simplex with the rectum ending blindly at the proctodaeum.

The views of the fate of the embryonic cloaca are still conflicting. The generally-accepted view of the division of the cloaca, by downgrowth of a

uro-rectal septum into a ventral urogenital and a dorsal rectal portion, is strongly opposed by the comparative and embryological evidence brought forward by Wood-Jones ('04), who maintains that the cloaca forms the urogenital sinus only, the rectum being developed as a new outgrowth (postallantoic gut) from the primitive hind gut. Recent work by Pohlman ('11), Buchanan and Frazer ('18) support the former view, and such a view is apparently sufficient to explain the case represented in fig. 8. But this view fails to explain the commonest condition—that in which recto-urethral fistula accompanies imperforate anus. Retterer (1890) describes the separation of the cloaca by two lateral cloacal folds which grow medially and fuse. Zucker-

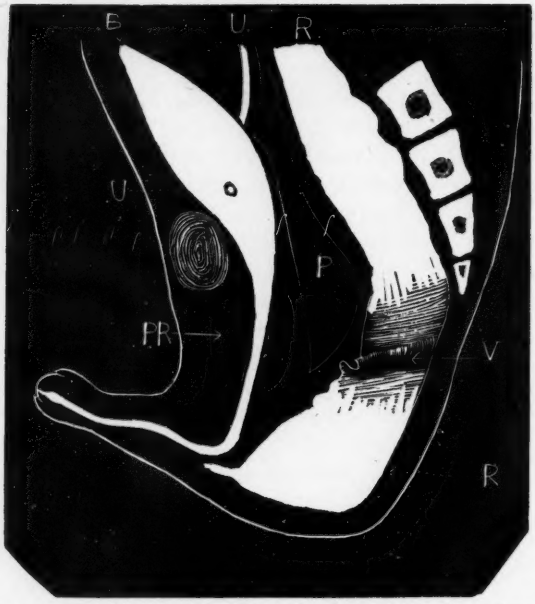

Fig. 8. Imperforate anus. *B.* bladder; *U.* ureter; *P.R.* prostate; *P.* peritoneal cavity; *R.* rectum; *V.* main valve of Houston.

kandl ('08) states that the division of the cloaca is accomplished by three folds, a median (uro-rectal) and two lateral, which eventually obliterate the triradiate space between their free borders. Either of these two views, by supposing incomplete fusion of the septa, will explain the persistence of a communication between the two derivatives of the cloaca. Such a view would necessitate a wide degree of variation in the position of the fistulous communication.

According to Wood-Jones, the recto-urethral fistula is a persistence of the cloacal anus of the early embryo—comparable to the cloacal anus of Echidna. This cloacal anus which is doomed to be exchanged for the definitive anus of the adult is bounded cranially by that sheet of recto-cloacal muscle which

can be recognised in every adult pelvis as the recto-urethral muscle, and marks the most caudal limit of the peritoneal cavity in the recto-vesical pouch, which is of great depth in the foetus. In the adult, the recto-urethralis muscle consists of longitudinal fibres of the rectum which sweep downwards and forwards to the apex of the prostate and reascend in the muscular coat of the prostatic urethra (Elliot Smith '08). The main rectal valve of Houston (fig. 8) serves to demarcate the site of this early embryonic communication.

Thus this case of atresia ani serves to illustrate the need for a comprehensive examination of the development of the hind-end of the body.

The testicles are situated at the internal abdominal rings and their progress through the abdominal wall has commenced, as is shown by the extension of the gubernacula along the inguinal canals. The right kidney, suprarenal and ureter are normal, but there is no trace of the left kidney, left ureter or left renal vessels. The left suprarenal is present. Both suprarenals and the right kidney are free from any abnormality of size and position, though the left suprarenal exhibits some alteration in shape owing to the absence of the left kidney. The trigonum of the bladder presents a patent right ureteric orifice but there is no trace of the left. The urethra and prostate are normal.

The absence of one kidney is a matter of interest to the surgeon and its occurrence is as frequent as that of imperforate anus, roughly one in 5000. Previous to the masterly analysis of Sir Henry Morris, the observers failed to differentiate clearly between entire absence of one kidney, congenital atrophy of one kidney and fusion of two kidneys. The statistics of Thompson ('13) and Gladstone ('14) show that the left kidney is absent about twice as often as the right, and that deformities of the urogenital organs are not the only congenital defects which may accompany the condition. The corresponding suprarenal is present in 90 per cent. of the cases in which one kidney is absent.

The right kidney in this case is normal in size, position, and blood supply, definitely disproving the statement frequently reiterated that a single kidney always exceeds the normal in size (Craven Moore, Gladstone). As Morris says, "an unsymmetrical kidney, like a renal mass composed of two kidneys fused together, may be either of much greater magnitude than the normal kidney, or not at all in excess of the normal." The question of hyperplasia versus hypertrophy of the glomerular elements has been discussed by Galeotti and Santa ('02), Eckardt (1888), Moore ('06) and Boycott ('10–'14).

The Wolffian duct reaches the cloaca in the 4 mm. embryo (Mall) and presents no traces of the renal bud. The renal bud appears near the termination of the Wolffian duct in the 5 mm. embryo. Thus the upgrowth of the renal bud to form the ureter and kidney occurs between the 4·5 and 5 mm. stage and proceeds so rapidly that the hilum of the kidney reaches its adult position by the end of the second month. Suppression of one kidney appears to be due to failure of the outgrowth from the hind end of the Wolffian duct, with the

result that the ureteric orifice is absent although the testis, vas, and ejaculatory ducts may be normal. Gladstone says that "congenital absence of the kidney and ureter is in all probability due to an arrest in the development of the distal end of the Wolffian duct and to a failure in its union with the cloaca." This explanation will not account for the presence of a normal testis and vas deferens in this case.

As Felix ('12) has shown there is no close parallel between the segmentation of the mesonephros and the somatic segments; the condition is one of marked dysmetamerism. In the 2·5 mm. embryo the mesonephros extends from the second to the fourth thoracic segments with eight well-developed tubules. In the 4·25 mm. embryo the mesonephros extends from the seventh cervical to the second lumbar segment and contains 28 tubules. Thus the mesonephros grows both caudally and cranially. The cranial growth is completed in an

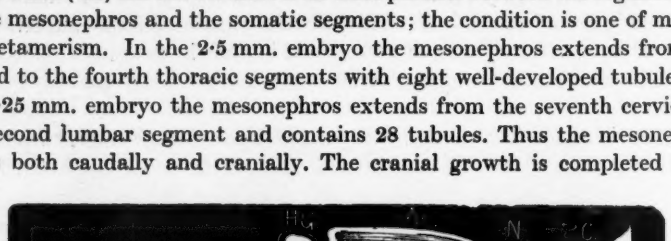

Fig. 9. Reconstruction of the arteria umbilicalis in a human embryo 5·3 mm. long. The umbilical artery is seen to arise from the aorta by three roots, a visceral and two parietal (after Felix, 1910). *Ao.* aorta; *U.A.* umbilical artery; *H.G.* hind gut; *Cl.* cloaca; *A.* allantois; *W.D.* Wolffian duct; *R.B.* renal bud; *N.* notochord; *S.C.* spinal cord.

embryo of 5·3 mm. (at the fifth cervical) and the caudal growth in an embryo of 7 mm. (at the third lumbar). Immediately the cranial growth is completed, degeneration sets in at the cranial end, so that ultimately the mesonephros is limited to the lumbar segments.

The ureteric bud appears at first between the 4·5 mm. and 5·3 mm. stage on the dorsal wall of the Wolffian duct and then inclines more and more towards its medial surface (Felix '12). This secondary medial position is of importance from the comparative point of view, since it persists throughout life in the marsupials and in these forms is an obstacle to the union of the two Müllerian ducts (Keibel 1896). At this stage (fig. 9) the Wolffian duct lies between the visceral (primary) and parietal (secondary) roots of the

umbilical artery. Persistence of the visceral root will offer a serious hindrance to the development of the ureteric bud for, as is well shown by the clinical history of arterial aneurism, every tissue has to give way to an expanding artery. Therefore it is suggested that persistence of the primary visceral root of the umbilical artery may prevent the development of the renal bud. This still leaves one faced with the difficulty of accounting for the persistence or late disappearance of this visceral root.

In the 1·38 mm. embryo (Kroemer-Pfannenstiel) the umbilical artery arises by several roots in common with the vitelline arteries at the level of the fourth cervical segment, and migrates caudally to reach the fourth lumbar segment at the 5·3 mm. stage when both visceral (primary) and parietal (secondary) roots exist for a short time coincidently, so as to form an arterial ring enclosing the Wolffian duct (Keibel and Elze '08). Thus, during their caudal migration, the umbilical arteries must have passed over those segments, eighth and ninth thoracic, which show complete suppression on the left side, as displayed by the absence of the two half vertebrae, eighth and ninth ribs, and eighth and ninth thoracic nerves. One is tempted to suggest that this foetus, somewhere near the 4·5 mm. stage, was subjected to an arrest in development in the precartilaginous stage which led to defective development of the heart, great vessels and lungs, defective development of the left half of the eighth and ninth thoracic segments, defective development of the left kidney, and defective development of the cloacal membrane. The obvious objection to the above is the disposition of the vascular, lung, renal and upper limb anomalies to the left side of the body, whereas the umbilical artery is defective on the right side. The primitive defect of segmentation may be closely associated with an exaggeration of that degree of asymmetry of the embryonic axis which von Baer described almost a hundred years ago as a normal characteristic of the embryo.

My thanks are due to Mr Bendit, of University College Hospital, who procured the specimen: to my colleagues in the Anatomy, Radiographic and Gynaecological Departments who have been my ready helpers; and to Mr Gerrard, of the Slade School of Art, who has devoted much labour to the preparation of the wood-cuts.

Addendum

Opportunity has recently been afforded for the examination of a full-term male baby aged three weeks of the same parentage. The baby presents buphthalmia, bilaterally symmetrical nævi of the naso-facial angle and hypospadias. This confirms the ancient dictum that the mother who gives birth to a merosomatous monster is more likely to give birth to another merosomatous monster than to a normal child.

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REVIEW

A Laboratory Manual for Comparative Vertebrate Anatomy. By LIBBIE H. HYMAN. The University of Chicago Press. Chicago, Ill.

There may be conflicting views concerning the method of inculcating the facts of comparative vertebrate anatomy but there can be little doubt that Dr Hyman has rendered a service to practical zoology the world over in the publication of this book which represents the outcome of a successful and efficient working of the "system by system" plan over several years in a large university.

This "comparative" method, although commended from the theoretical point of view, is generally scouted as unworkable on the grounds of its prodigal demands in material. The experience at Chicago has exposed the falsity of the contention. It now remains to be seen whether this local success will affect the general teaching of zoology in America and in the British Empire. A firmly-grounded trust in the well-tried "type" method and a staunch adherence to tradition are the factors which are likely to militate against the widespread use of the text-book in this country.

The treatment is generally well-balanced, its tone illustrating admirably the intensity of the American scholastic method. One feels however that a sensitive spirit will recoil at finding such statements as "the liver *is compelled to* grow into the septum" or "The two pleural cavities.....*split* the pericardium from the ventral body wall." An earnest effort is made to render clear the ever-elusive body cavities and the circulatory system is enriched by the recent publications of Huntington and McClure, but the central nervous system is presented as inadequately as in the majority of zoological text-books and the word "visceral" has worked its usual havoc in the nervous, skeletal and muscular systems. When shall we hail the day of its disappearance along with the three specific germ layers, the endodermal origin of the segmented mesoderm, the ectodermal origin of neuroblastic tissue, the archenteric coeloma—all that dogmatic crew which have hitherto manned the zoological ship of state?

The pictures are schemata for the most part, but there is design in this treatment, the student being expected to make drawings from his own preparations—a practice greatly to be commended. Whether he should be relieved of making his own summaries is another matter.

In providing a suitable glossary, important direct practical hints and an ample index, the author has afforded addenda which are frequently overlooked in texts of this nature. Here is a worthy addition both to the student's bookshelf and to the teaching of comparative anatomy.

R. A. D.